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The Eriocaulaceae of Peru: Three Taxonomic Novelties, and a Revised Checklist with Key

Nancy Hensold



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Cover: Inflorescence of *Paepalanthus piscatorum* var. *piscatorum* in San Martín, Peru (Voucher: J. L. Clark 11797).
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The Eriocaulaceae of Peru: Three taxonomic novelties, and a revised checklist with key

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Abstract

Paepalanthus piscatorum, sp. nov. (*P.* subsect. *Polyactis*) is described with two varieties endemic to the eastern Andes in Peru and Ecuador. *Paepalanthus dichotomus* var. *glabrescens* Moldenke is raised to species status as *Paepalanthus glabrescens* comb. et stat. nov. (*P.* subsect. *Dichocladus*), endemic to the vicinity of Chachapoyas. Affinities and floral morphology of both species are discussed in detail. The variability in *Syngonanthus peruvianus* is documented, with an updated species description. *Paepalanthus stuebelianus* is placed in synonymy of *P. intermedius*. In addition a revised checklist for Peru is presented, updating the account in the *Catalogue of the Flowering Plants and Gymnosperms of Peru* (1993), and providing global habitat and distribution information, general comments on phytogeographic patterns in the family, and a dichotomous key to Peruvian species. Images of representative specimens are provided in a supplementary online resource (<http://fieldmuseum.org/fieldiana-hensold>). The new total of 31 species reflects 13 new taxon records, three deleted species records, three name changes due to synonymy, and several changes in distributional records. Ten endemic taxa are reported, for which conservation status is provisionally assessed for eight, according to the International Union for Conservation of Nature guidelines. Four taxa were found to be widely disjunct from white sand areas of northern South America.

Resumen

Paepalanthus piscatorum sp. nov. (*P.* subsect. *Polyactis*) se describe con dos variedades, endémicas de la parte de los Andes orientales en el Perú y Ecuador. *Paepalanthus dichotomus* var. *glabrescens* Moldenke se eleva a nivel de especie como *P. glabrescens*, comb. et stat. nov. (*P.* subsect. *Dichocladus*), endémico a la zona de Chachapoyas. Se discuten las afinidades y la morfología floral de ambas especies en detalle. Se documenta la variabilidad en *Syngonanthus peruvianus*, con una descripción de la especie actualizada. *Paepalanthus stuebelianus* está colocado en la sinonimia de *P. intermedius*. Además se presenta una lista revisada de las ericauláceas del Perú, actualizando el *Catálogo de las Angiospermas y Gimnospermas del Perú* (1993), incluyendo la información del hábitat y distribución global, observaciones generales sobre los patrones fitogeográficos en la familia, y una clave dicotómica para especies peruanas. Imágenes de especímenes representativos se proporcionan en un recurso suplementario disponible en línea (<http://fieldmuseum.org/fieldiana-hensold>). El nuevo total de 31 especies refleja 13 nuevos registros de taxones, tres registros de especies eliminadas, tres cambios de nombre debido a la sinonimia, y varios cambios en registros de distribución. Se reportan diez taxones endémicos, y el estado de conservación se evalúa provisionalmente para ocho, de acuerdo con las directrices de la UICN. Se encontraron cuatro taxones que están ampliamente disjuntos de las zonas de arena blanca de la parte norte de Sudamérica.

Introduction

The Eriocaulaceae are a family of herbaceous monocots characteristic of open, wet, sandy, or otherwise acidic nutrient-poor sites in the tropics. Of about 1200 known species, about 800 are neotropical, and of these, about 600 are endemic to Brazil and Venezuela, especially in association with outcrops of the Brazilian and Guiana Shields (Hensold, 2008; Giulietti, 2015; Sano et al., 2015). According to the most recent checklists and catalogues, only about 69 species are reported from the western South American countries of Colombia, Ecuador, and Peru, including about 30 endemic to the Andes (Brako & Hensold, 1993; León-Yáñez & Hensold, 1999; Giulietti, 2015). In the *Catalogue of the Flowering Plants and Gymnosperms of Peru*, and its published updates (Brako & Hensold, 1993; Vásquez & Rodríguez, 2002; Ulloa Ulloa et al., 2004), five genera and 22 species of Eriocaulaceae are listed for Peru, including four endemic species and one endemic variety. Conserva-

tion status of some endemic taxa was evaluated by Monsalve and León (2006), following the International Union for Conservation of Nature (IUCN) standards.

With the influx of new collections in recent years, especially from the eastern Andes and Amazon Basin, the number of recorded species has substantially increased, together with a better understanding of natural variation of existing taxa. Watanabe et al. (2015a, b) recently described two new Amazonian species of *Syngonanthus* Ruhland, both occurring in Amazonian southern Peru and previously treated as a single species. Hensold (2016) resolved a complex of three high-elevation cushion plant species of *Paepalanthus* Mart. with a long collection history in Peru, which had also previously been treated as a single species. Additional adjustments and updates to the taxonomy of Peruvian Eriocaulaceae, including detailed taxonomic observations of three taxa, are here provided. The resulting checklist is based on my own specimen observations, with the exception of the five species of *Paepalanthus* subg.

Platycaulon Körn., which are here treated only provisionally. This subgenus was the subject of a preliminary monograph by Tissot-Squalli (1997a,c), who also described two species new to Peru (1997b). That treatment is followed here, but the taxonomy of the Andean species, all of which belong to *Paepalanthus* sect. *Conferti* (Ruhland), stat. nov., remains problematic, and most material is undetermined. The group is currently under study by other workers.

Materials and Methods

A total of 302 specimens from Peru were examined, mostly from the herbaria of the Field Museum (F), Missouri Botanical Garden (MO), and Universidad de San Marcos in Lima (USM). The specimens from USM were examined from photographs. Images of additional selected specimens from other herbaria were examined via JSTOR (2000 onward), the C. V. Starr Virtual Herbarium at New York Botanical Garden (<http://sweetgum.nybg.org/science/vh/>) and on request from Universidad Nacional de la Amazonia Peruana (AMAZ). Herbarium acronym usage follows Thiers (2015).

Vouchers of *P. ferreyrae* Moldenke and *P. muscosus* Körn. used for comparison with *P. glabrescens* (Moldenke) Hensold were cited by Hensold (2016, p. 4). Vouchers for *P. dichotomus* Körn. include the following specimens. Guyana: K. Wurdack 4135, and 5477, Maguire 40653. Venezuela. Bolívar: Maguire 33729, Steyermark & Wurdack 331, Steyermark 59209.

The flowers in Figures 4D–F were photographed with a Dino-Lite AM-413T USB Digital Microscope; those in Figures 4E–F were boiled and mounted in water. The seeds of *Paepalanthus* subsect. *Dichocladus* Ruhland (Fig. 2) were wet and re-dried to check for hygroscopic wall thickenings, then gold-coated and imaged by scanning electron microscope.

Global distribution and habitat information provided in the checklist is based on specimen observations at F and MO, and published or online floras and checklists (Hensold, 1999; Giulletti, 2015; Sano et al., 2015).

PART 1. TAXONOMIC NOVELTIES AND NOTES

Paepalanthus Mart.

Paepalanthus subsect. *Dichocladus* Ruhland

Paepalanthus glabrescens (Moldenke) Hensold, comb. et stat. nov.

Figures 1, 2A

Paepalanthus dichotomus var. *glabrescens* Moldenke, Phytologia 9: 187. 1963. TYPE: Peru. Amazonas: Prov. Chachapoyas, 1–5 km W of Molinopampa, 2400–2450 m, 18 Jul 1962 (post-fr), J. J. Wurdack 1388 (holotype, US; isotypes, F, GH, K, LL, NY, P, S).

DESCRIPTION—Perennials forming rounded cushions only a few centimeters tall, the branchlets densely leafy, the branching sympodial, often pseudodichotomous; roots wiry, sometimes slightly tortuose. Leaves linear-subulate, broadly amplate at base, 3–5 mm long, 0.65–0.8 mm wide just above the amplate sheath and tapered to *thick, bluntly cuspidate apex*, coriaceous, the margins rounded and *midvein prominently thickened abaxially*, the midvein thickening extending to the apical margin, glabrous except for the long-ciliate

sheathing bases. *Tubular peduncle sheaths lacking*. Peduncles solitary at branch apex, 1.2–10 mm long, prominently *3-costate* to the apex, pubescent with flattened, twisted basifixed (or partly dibrachiate?) hairs. Capitula 3–4 mm wide, *campanulate* at maturity, the receptacle strongly concave. *Involucral bracts few, in only about 2 series, the lower bracts as large as the upper*; all bracts brown, coriaceous, glabrous or tufted at abaxial apex, glabrous within. Receptacular bracts cream to light brown, broadly linear-spatulate, convex-acute, densely long-plumose on upper margins and back, the tuft ca. 1.0 mm long at tip. Staminate flowers: Sepals blackish-brown, grading to pale gray-brown or coppery-brown below, connate at base in a narrow tube about $\frac{1}{4}$ their length, lobes spatulate, obtuse, or rounded, with a thick tuft of smooth white subacute trichomes at upper margin and abaxial apex; corolla with slender anthophore about equalling the tubular portion in length, hyaline, blackish-tinged, glabrous, shallowly lobed, not evidently involute after anthesis; anthers cream, ca. 0.3–0.35 mm long. Pistillate flowers: Sepals colored as in staminate flowers but paler toward base, ligulate, obtuse to truncate-emarginate, elongating and recoiling hygroscopically from the tips in fruit; *petals narrow, sublinear, obtuse, ca. 0.15 mm wide*, broadened slightly at base, the upper margins of adjacent petals *not imbricate* at anthesis or enfolding styles, tufted with scattered spreading hairs near tip. *Nectaries dark-pigmented* with finger-like papillae, and both *these and the dark stigmas robust and protruding prominently from capitulum* especially in fruit. Style base narrowed, not thickened. Seeds ca. 0.55–0.6 mm long, *primary sculpture of smooth, narrow longitudinally elongated cells* with slightly raised margins; pseudotricones or other anticlinal wall thickenings absent.

PHENOLOGY—Collected in flower March to May, early in the dry season. The type collected in July is past fruiting.

HABITAT AND DISTRIBUTION—Endemic to Dist. Chachapoyas, Amazonas Region, Peru, in the watershed of the upper Río Utcubamba, elev. 2300–3100 m. Reported from scrub vegetation, on white sand, and in jalca.

CONSERVATION STATUS—Endangered B1ab(iii). Assessed as Critically Endangered by Monsalve and León (2006), who cited only one voucher, and noted the threat of human-set fires to the habitat. The species is now known from four collections, representing two localities about 75 km apart. This is still a small number from this well-collected area, and the critical status may be found more appropriate. This species occurs on dry, rocky sites, which may be relatively vulnerable to fire, in comparison to more abundantly collected Eriocaulaceae growing on wetter sites in the same province (*Paepalanthus intermedius* Körn., *Syngonanthus peruvianus* Ruhland).

DISCUSSION—*Paepalanthus glabrescens* was originally described as a glabrous-leaved variety of *P. dichotomus* Klotzsch ex Körn., a common species of the Guiana Highlands in Venezuela and Guyana. It is also similar to two Andean species, *Paepalanthus ferreyrae* Moldenke, of northern Peru, and *Paepalanthus muscosus* Körn., of Andean Colombia and Venezuela. These four species may be referred to *P.* subsect. *Dichocladus* Ruhland (1903; type *P. dichotomus*), a group originally distinguished by its subdichotomously branched cushion habit. Study of herbarium material also revealed floral and seed characteristics uniting this group of four species, with their similarities summarized as follows:

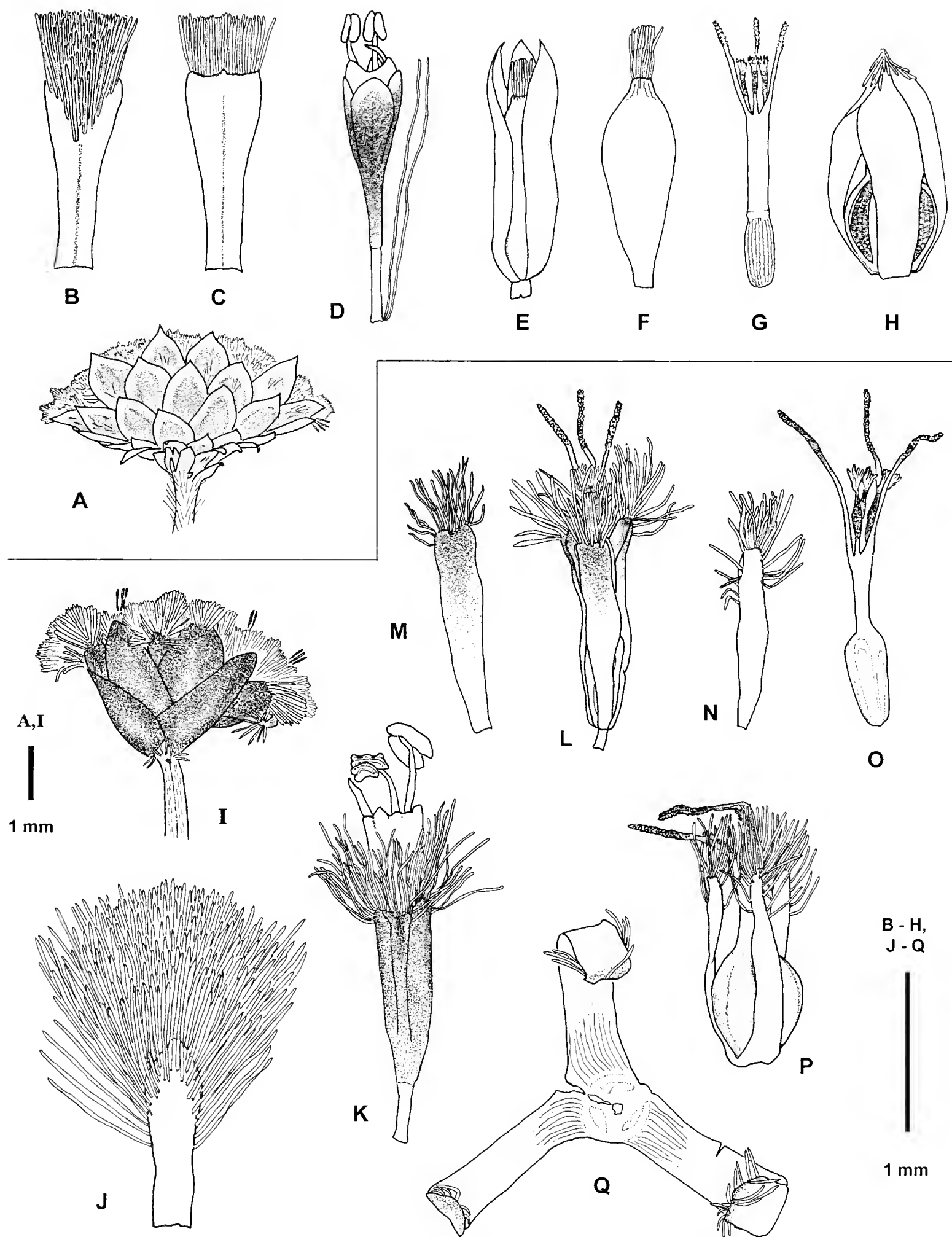


FIG. 1. Capitula and flowers of *Paepalanthus dichotomus* and *P. glabrescens*. (A–H) *Paepalanthus dichotomus*. (A) Capitulum. (B) Receptacular bract, abaxial. (C) Same, adaxial. (D) Staminate flower. (E) Pistillate flower. (F) Petal, pistillate flower. (G) Gynoecium. (H) Diaspore, with petals. (I–Q) *Paepalanthus glabrescens*. (I) Capitulum. (J) Receptacular bract, abaxial, margin outlined with dotted line. (K) Staminate flower, one fallen anther. (L) Pistillate flower. (M) Sepal, pistillate flower, abaxial. (N) Petal, pistillate flower, adaxial. (O) Gynoecium. (P) Diaspore, with petals. (Q) Fruiting calyx, abaxial, from below. (A, K. Wurdack 4135; B–H, K. Wurdack 5477; I–J, van der Werff 14940; K–Q, van der Werff 16912.)

Habit pulviniform, with pseudodichotomous branching, the stems covered by small stiff subulate leaves. Pistillate flowers with sepals recoiling hygroscopically from the tip in fruiting (Fig. 1Q); petals tufted with trichomes at apex, oth-

erwise glabrous; stigmas simple; nectaries (stylar appendages) red-brown below with a hyaline long-papillate mouth; seeds reticulate, cells of the seed coat with raised margins, but lacking pseudotrachomes (localized columnar wall thickenings).

Label data suggest that all four species prefer sandy or rocky sites. *Paepalanthus glabrescens* and the other two Andean species are rarely collected local endemics, reported from 1600–3100 m, while *P. dichotomus* is a common species of white sand savanna in Venezuela and Guyana, from 500–2100 m. This contrasts with the habitat preferences of a second group of Andean cushion plants, including *Paepalanthus pilosus* (Kunth) Kunth and relatives, which occurs from about 1800–4000 m, on poorly drained, peaty sites. The latter group was recently revised and included in an emended *Paepalanthus* subsect. *Cryptanthella* Suess., and the morphological differences distinguishing this complex from *P.* subsect. *Dichocladius* discussed (Hensold, 2016).

Of these four species, *P. glabrescens* is the most divergent morphologically, as summarized in the first couplet of this key to species:

- 1 Tubular peduncle sheath absent. Leaves firmly cuspidate, without evidence of a hydathode, the midvein thickened abaxially, the lamina glabrous. Peduncles prominently 3-ribbed to the apex. Capitula campanulate throughout anthesis. Involucral bracts few, large, in about 2 series, the lowest (outermost) nearly equal the inner in size. Pistillate flowers with petals linear, non-imbricate, ca. 0.15 mm wide, tufted with spreading hairs at tip, non-imbricate at anthesis; nectaries and stigmas thick, darkly pigmented, the stigmas still exert after anthesis. Seed coat of small, longitudinally elongate cells. *P. glabrescens*
- 1' Tubular peduncle sheaths present, robust, leaf-like, long-ciliate in the sinus. Leaves rounded to subtruncate, with evidence of an apical hydathode; the abaxial midvein neither thickened nor prominent; pubescence of the lamina variable but usually present along the margins, on the adaxial surface, and sometimes on the abaxial midvein. (Glabrous leaf blades are found only in specimens of *P. dichotomus* var. *glabrescens* Moldenke from Chimantá Massif, Venezuela.) Peduncles smooth, terete near the apex, sometimes obscurely angled to narrowly furrowed up to at least 1 cm below the apex, never with thickened ribs. Capitula at maturity discoid to hemispheric, with a flattened base. Involucral bracts in at least 4 series, the lowest (outermost) bracts mostly half or less the size of the uppermost bracts. Pistillate flowers with petals oblong-elliptic to spatulate, 0.35–0.45 mm wide, ciliate at upper margin, the distal margins overlapping at anthesis. Nectaries and stigmas pale and membranous, not evident on surface of capitulum, shriveling and retracted within petal hairs after anthesis. Seed coat with cells large, approximately isodiametric. 2
- 2 Involucral bracts and sepals dark brown at anthesis, pubescent. *P. ferreyrae*
- 2' Involucral bracts glabrous, scarious, with hyaline margins. . . . 3
- 3 Involucral bracts lanceolate, acute; sepals of pistillate flowers rounded and brown at apex, pale below; style tapered to base; seeds smooth. *P. muscosus*
- 3' Involucral bracts ovate to obovate, mucronate; sepals of pistillate flowers sharp-acute, pale throughout; style columnar; seed surface indented, obscurely pitted. *P. dichotomus*

The hydathode in the latter three species is evidenced by a small apical notch, often flanked by tufts of trichomes, a whitish subapical tissue mass visible below the epidermis, or in older leaves a small subapical pit on the abaxial surface. The

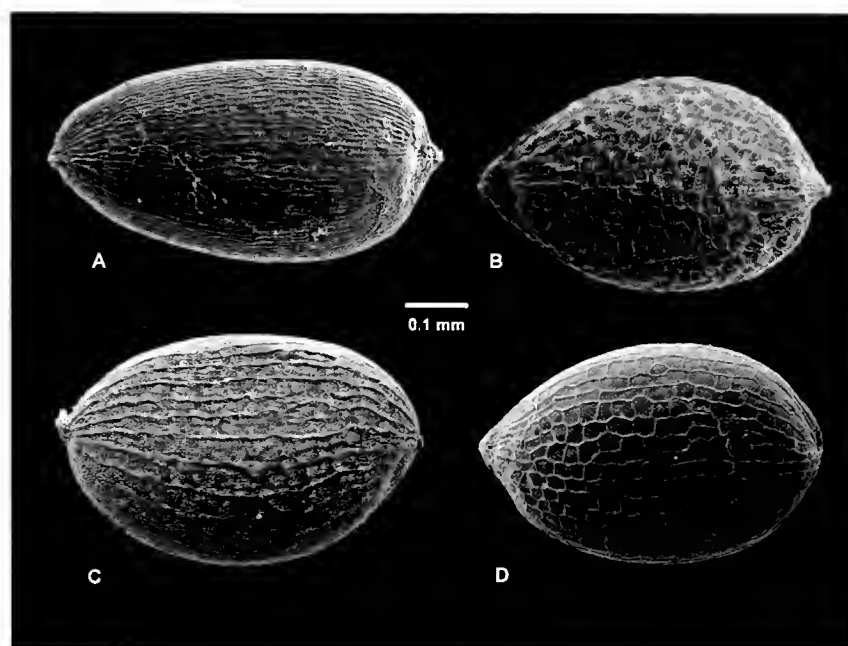


FIG. 2. Seeds of selected species of *Paepalanthus* subsect. *Dichocladius*. (A) *Paepalanthus glabrescens* (Sagástegui 7454). (B) *Paepalanthus dichotomus* (K. Wurdack 5477). (C) *Paepalanthus muscosus* var. *tachirensis* Moldenke (Maas & Tillett 5282). (D) *Paepalanthus ferreyrae* (Sanchez 10020).

smooth coriaceous cuspidate leaf tips of *P. glabrescens* do not suggest the presence of hydathodes.

The lack of a tubular peduncle sheath (or “spathe”) in *P. glabrescens* is particularly unusual. These are almost always present in Eriocaulaceae, though occasionally reduced or leaf-like in species with very short peduncles. The axillary inflorescences of *Tonina fluviatilis* Aubl. lack sheaths, but a normal foliage leaf occurs at the peduncle base in an adaxial position, homologous to a prophyll. Similarly, in *Syngonanthus cuyabensis* (Bong.) Giul. et al., the short-peduncled inflorescences in terminal clusters lack tubular sheaths but are also associated with foliage leaves in an adaxial position (Giulietti et al., 2012). In *P. glabrescens* no vestige of a reduced tubular sheath is found, even in young inflorescences in bud, but since the inflorescences are terminal, the reversion of a sheath to a normal foliage leaf might be impossible to detect.

The seeds of all four species are unusual compared to others studied in the genus. Transversely elongate cells in longitudinal files are the most common condition in *Paepalanthoideae* Ruhland, and irregular or rod-like thickenings of the anticlinal walls (“pseudotrichomes”) are found in the majority of *Paepalanthus* species studied (e.g., Giulietti et al., 1988; Hensold, 1988; Kraus et al., 1996; Scatena & Bouman, 2001). However, in *P. dichotomus*, *P. ferreyrae*, and *P. muscosus* the seed coats are composed of irregular isodiametric polygonal cells, with slightly thickened or raised margins (Fig. 2B–D), and granular deposits sometimes present (Fig. 2B,C). *Paepalanthus dichotomus* is distinct for its obscurely ridged or pitted seed surface, the raised irregular ridges not aligned with the epidermal cell outlines and presumably either originating in cells of the inner integument or as the result of deformation due to shrinkage. A similar condition is otherwise only reported in *Comanthera* L. B. Sm. subg. *Comanthera* (Barreto et al., 2013). *Paepalanthus glabrescens* itself is very unusual for its seed coat composed of cells with the long axis oriented longitudinally, and these are unusually narrow, only about one-third the width of the cells in the other three observed species of the subsection (Fig. 2A). The only other report in the family of cells

elongated parallel to the long axis of the seed is *Eriocaulon truncatum* Mart. of India (Nair, 1987), which has much broader sub-isodiametric cells. None of the species sampled here had pseudotrachomes or other localized thickenings of the anticlinal walls.

In fruit, these species have a thickened hygroscopic calyx (Fig. 1Q), which flattens outward and recoils at the tips upon drying to eject the diaspore. This is similar to the fruiting calyx in *P.* subg. *Platycaulon*, associated with a “catapult dispersal mechanism” (Trovó & Stützel, 2011). This calyx morphology is best known from *P.* subg. *Platycaulon* and *P.* subg. *Xeractis* Körn., groups characterized by bifid style branches, but is also reported for some species with simple stigmas, including *P. sessiliflorus* Körn. (Körnigke 1863, t. 48.I), and *P. lamarckii* Kunth (Meikle & Baldwin, 1952, fig. 27).

Of the species here compared, *P. glabrescens* is slightly more similar to *P. ferreyrae*, due to the dark brown, pubescent involucre bracts, and similar pubescence and color of the sepals. *Paepalanthus ferreyrae* is also its nearest geographic neighbor, occurring just to the north, in the Río Imaza watershed in Amazonas, Peru, and in Cajamarca. The allopatric distribution pattern of these two putative relatives is similar to that seen in the sister species *P. intermedius* and *P. piscatorum* Hensold, discussed below.

Paepalanthus subsect. *Dichocladus* is also known from lowland Amazonian sand savannas in Venezuela (e.g. *Paepalanthus aristatus* Moldenke; Hensold, 1991) and disjunctly in Minas Gerais, Brazil (*Paepalanthus bonsai* Trovó & Sano, *Paepalanthus glaziovii* Ruhland), but these species were not closely examined here. Recent cladistic analysis of *Paepalanthus* included only Brazilian species of *P.* subsect. *Dichocladus* (Trovó et al., 2013). However, these differ from species of the Andes and northern South America by the bifid stigmatic branches, so molecular analysis would be useful to confirm the relationship.

ADDITIONAL SPECIMENS EXAMINED: **PERU**. Amazonas: Prov. Chachapoyas, Jalca de Calla Calla, 3100 m, 7 May 1970 (fr), *A. Sagástegui* A. 7454 (F); a few km from Molinapampa, on white sand, 14 Mar 1998 (fl), *H. van der Werff* et al. 14940 (F, MO); near Molinapampa, 2100–2500 m, 10 Apr 2001 (fl), *H. van der Werff* et al. 16912 (F, MO).

***Paepalanthus* subsect. *Polyactis* Ruhland**

***Paepalanthus piscatorum* Hensold, sp. nov.**

Figures 3–5

TYPE — Peru. Cajamarca: Prov. San Ignacio. Near San José de Lourdes, Llanos, forest remnants, peat bog, and open jalca area over sandstone; in marshy areas, 1900–2100 m, 10 June 1998 [anthesis], *M. Weigend*, *Th. Franke*, *J. Skrabal* & *M. A. Gonzales B.* 98/498 (holotype, F; isotypes, M 0011876, CPUN n.v., HUT n.v., USM n.v.).

DIAGNOSIS — Caules ad 1.6 m longi, graciles, ubique foliosi, cavi, proxime infra apices floriferos ramificantes. Inflorescentiae 5–30 (–80) terminaliter fasciculatae. Folia lanceolata ciliata, apice acuta argute cuspidata vel aristata, vaginis basalibus clausis. Flores trimeri; sepala fusca comosa trichomatibus obtusis plerumque tuberculatis. Flores masculi: tubus corollae 6-loba, lobis interstaminalibus ciliatis. Flores feminei: corolla extus dense plumosa trichomatibus longis rectis; gynoeceum stigmatibus simplicibus et appendicibus papillosis.

DESCRIPTION — Plants with long, weak, sparsely branched, uniformly leafy stems to 1.6 m long, 2–6 mm in diame-

ter, hollow at maturity with a woody cortex, erect-ascending or sprawling on other vegetation, often decumbent at base, sometimes sprouting from the base but not evidently rhizomatous, lacking a basal rosette, producing terminal inflorescences flanked by 1–5, commonly 2, subapical, ascending lateral branches, these often initiated while the primary umbel is still in flower and soon overtopping it; the lateral branches reaching 9–15 cm in length, mostly producing terminal umbels as well, followed in more robust specimens by a third order of flowering or sterile branches; stems not otherwise branched. Stems glabrous or sparingly pilose when young, with an inconspicuous collar of scurfy thin-walled brownish hairs below each leaf base, glabrate with age. Leaves with basal sheath ca. 0.5–1.0 cm long, connate-amplexicaul ca. 1–5 mm of its length, the connate portion smooth, pale brown, brittle, glabrous; lamina lance-triangular, recurved and spreading, more or less conduplicate at least when dry, 1.7–6.0 cm long, 3–10 mm wide at base, 2–9 mm wide at midpoint, linear-tapering to acute apex, the abaxial surface finely white-striate, the adaxial uniformly green; pubescence of short to long cilia on margins, usually antrorse-appressed near apex, the abaxial and adaxial surfaces glabrous or with scattered weak appressed or subappressed hairs and then glabrate; leaf apex minutely callose-cuspidate to aristate, the arista up to 0.3 mm long, glabrous, slightly decurved, with the lamina just proximal to the callose tip subterete-thickened (probably hydathodal) in mature leaves (Figs. 4B, 5B), and densely bearded adaxially with thin-walled trichomes. Inflorescences in terminal umbelliform clusters of ca. 5–30 (–78). Peduncle sheaths 1.8–3.0 cm long, somewhat lax, obscurely striate, with an oblique opening, pubescent like the abaxial leaf surface; the apex rounded and papery-hyaline at the margins to foliaceous and occasionally cuspidate or aristate, ciliate at mouth, sometimes also tufted at adaxial apex. Peduncles ca. 5–15 cm long, 3–4 (–5) costate, pubescent with weak mostly appressed-ascending (few-celled) straight hairs, glabrate with age except at the apex where a sericeous collar of longer hairs subtends the involucre. Capitula 4–6 mm in diameter, broadly obconic to hemispheric at maturity. Involucre bracts in about 3 series, dark blackish-brown, or the outer bracts paler brown; all shiny, hyaline, and brittle when dry, or the outer bracts thickened along the midvein and then lighter brown than inner bracts; outer bracts triangular-ovate, cuspidate, grading to inner bracts oblong-obovate to subrotund, apiculate to aristate, body of the bract ca. 1.4–1.6 mm long × 1.2–1.5 mm wide, the arista up to 0.4 mm long but usually much shorter; all bracts long-ciliate on upper margins and usually also dorsally villous in upper third with flexuose sometimes early caducous trichomes. Floral bracts of the outer series transitional in shape between involucre bracts and inner floral bracts, the inner floral bracts broadly oblong- to linear-subspatulate to narrowly oblanceolate-spatulate, acute, 1.1–1.8 mm long, ca. 0.15–0.7 mm wide, blackish-brown, tufted with trichomes ca. 0.25–0.8 mm long at abaxial apex, about equalling or slightly surpassed by the sepals. Apical trichomes of floral bracts and sepals more or less contorted (not straight), the apical cells swollen, narrowly clavate, subacute to rounded, white due to inner wall ornamentation, often weakly tuberculate in outline. Flowers 3-merous, about 25–65 per capitulum, with sex ratio 1.0–2.7 staminate to pistillate, both sexes or only pistillate flowers found in outer whorl of capitulum. Staminate flowers: Pedicels 0.2–0.6 mm long, sparingly pilose, brittle when dry. Sepals blackish-brown, obrhombic to obovate- or oblanceolate-spatulate, acute to apiculate, 1.0–1.7 mm long ×

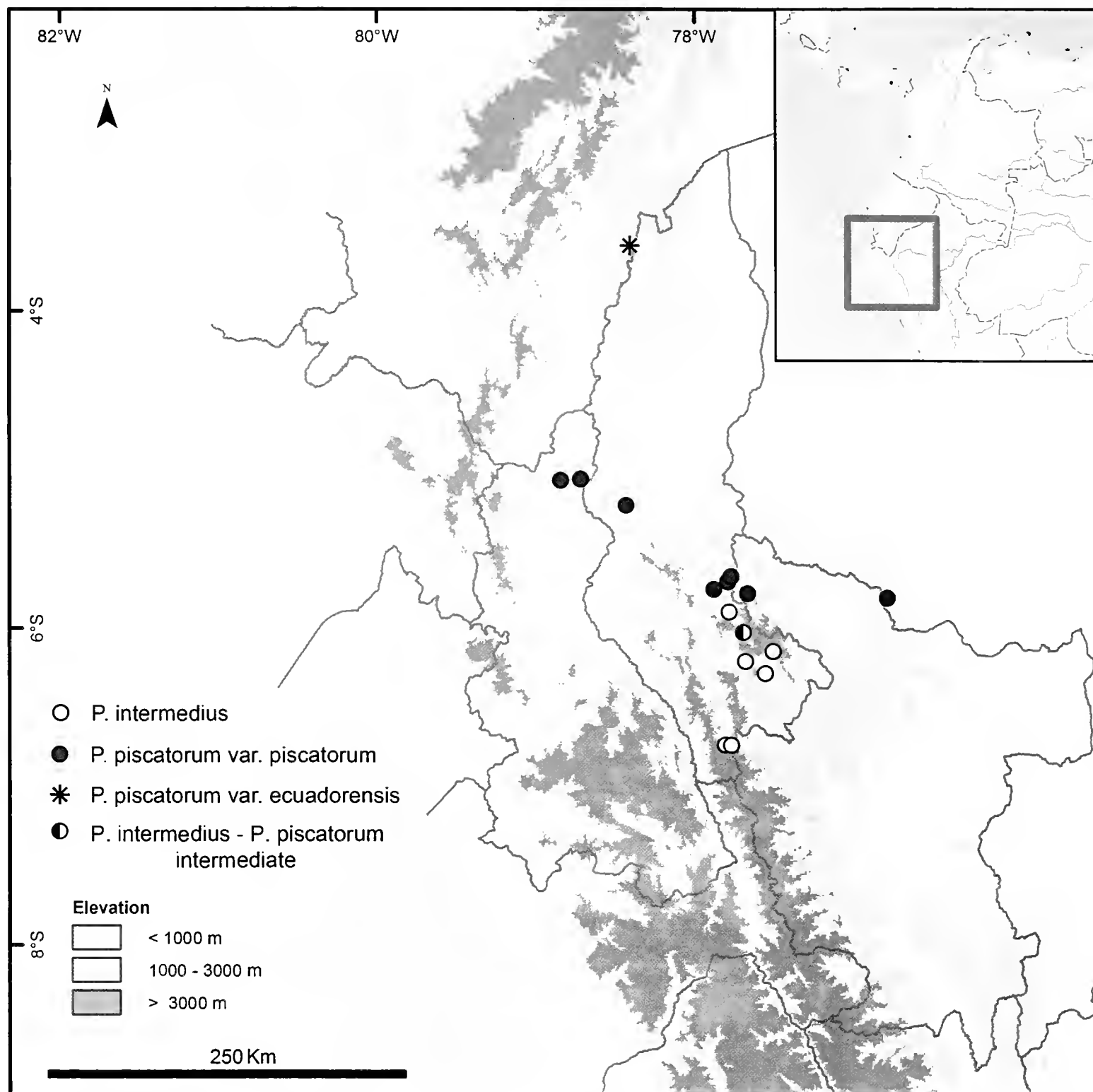


FIG. 3. Distribution of *Paepalanthus intermedius* and *P. piscatorum*.

0.3–0.65 mm wide, fused very shallowly up to 0.2 mm at base; the whole calyx slightly zygomorphic; sepals tufted abaxially at apex and ciliate at upper margins, glabrous within, the tuft 0.35–0.5 mm. Corolla with anthophore fleshy, linear (not obconic), half-equaling to equaling the tube, 0.4–1.0 mm long, the surface glandular with microscopic 1-celled globose trichomes; corolla tube (including lobes) 0.7–1.5 mm long, exsert from calyx ca. 0.3–0.5 mm at anthesis, the lobes 6, those opposite the staminal filaments narrow, acuminate, glabrous; the interstaminal lobes broader, rounded, irregular in outline, and ciliate with thin-walled obtuse trichomes; all lobes involute after anthesis. Anthers white, 0.30–0.35 mm at maturity, slightly exsert from corolla mouth; filaments adnate to base of corolla about 1/4 of filament length. Nectaries 0.40–0.55 mm, the papillose apex usually bright orange-red (as observed in dried material). Pistillate flowers: pedicels sometimes nearly obsolete, 0.03–0.33 mm, flattened, thin-walled, brittle when dry, sparingly and ephemerally pilose, easily separating from the sclerified calyx base at maturity. *Sepals* obovate-spatulate, with a broad base, acute to apiculate, $1.1\text{--}1.5 \times 0.35\text{--}0.8$ mm, be-

coming sclerenchymatous-thickened and lustrous spadiceous-brown only in the lower half, the apex and upper margins remaining thin, brittle, and blackish-brown, separating from corolla at maturity; trichome tuft 0.4–0.75 mm long. *Petals* oblong-linear to oblong-obovate, gradually tapered from the middle to the acute or subacute apex, $(0.85\text{--}) 1.2\text{--}1.6 \times 0.35\text{--}0.6$ mm; membranous at anthesis, usually dark-brown-tinged, like the sepals becoming thickened and lustrous brown along the lower midvein; densely and persistently bearded on the outer surface and margins from about 0.2–0.35 mm above the base, with a mass of long dense ascending plumose trichomes, the trichome apices linear-obtuse to narrowly clavate, exceeding the petals by 0.7–1.0 mm; only the thickened bases of the petals glabrous and visible externally; whole corolla from base to trichome tips $(1.7\text{--}) 1.8\text{--}2.35$ mm long, well-surpassing the calyx and detaching easily from it to disperse; petals not involute after anthesis. Staminal scales persisting within petal bases or at base of ovary septa, conspicuous, often callose thickened. *Ovary* 0.45–0.75 mm long, 3-locular, (but with some tendency to suppression or abortion of ovules to 1 or 2); style column

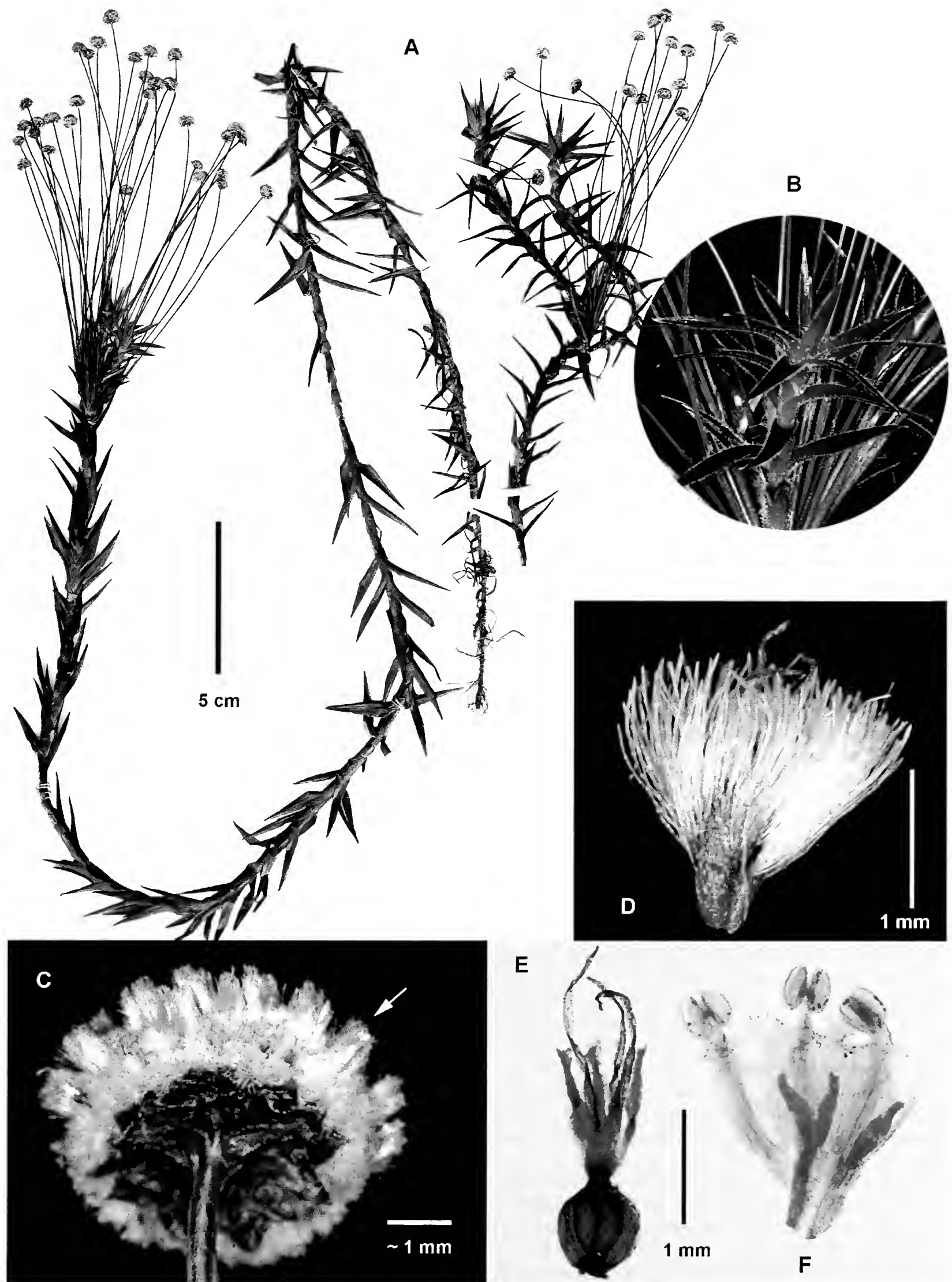


FIG. 4. *Paepalanthus piscatorum* habit, capitulum, leaves and flowers. (A) Whole plant, pressed. (B) Young branch. (C) Capitulum in fruiting condition; arrow indicates one of several emerging diaspores. (D) Immature diaspore, petals intact, sepals fallen. (E) Gynoecium with immature seeds, bright orange nectaries. (F) Staminate corolla, post-anthesis, with nectaries. (A,D, Weigend 98/498; B-C, Clark 11797; E, Neill & Quizhpe 15235; F, Perea 3629.) Photos 4B,C © J. L. Clark. Used by permission.

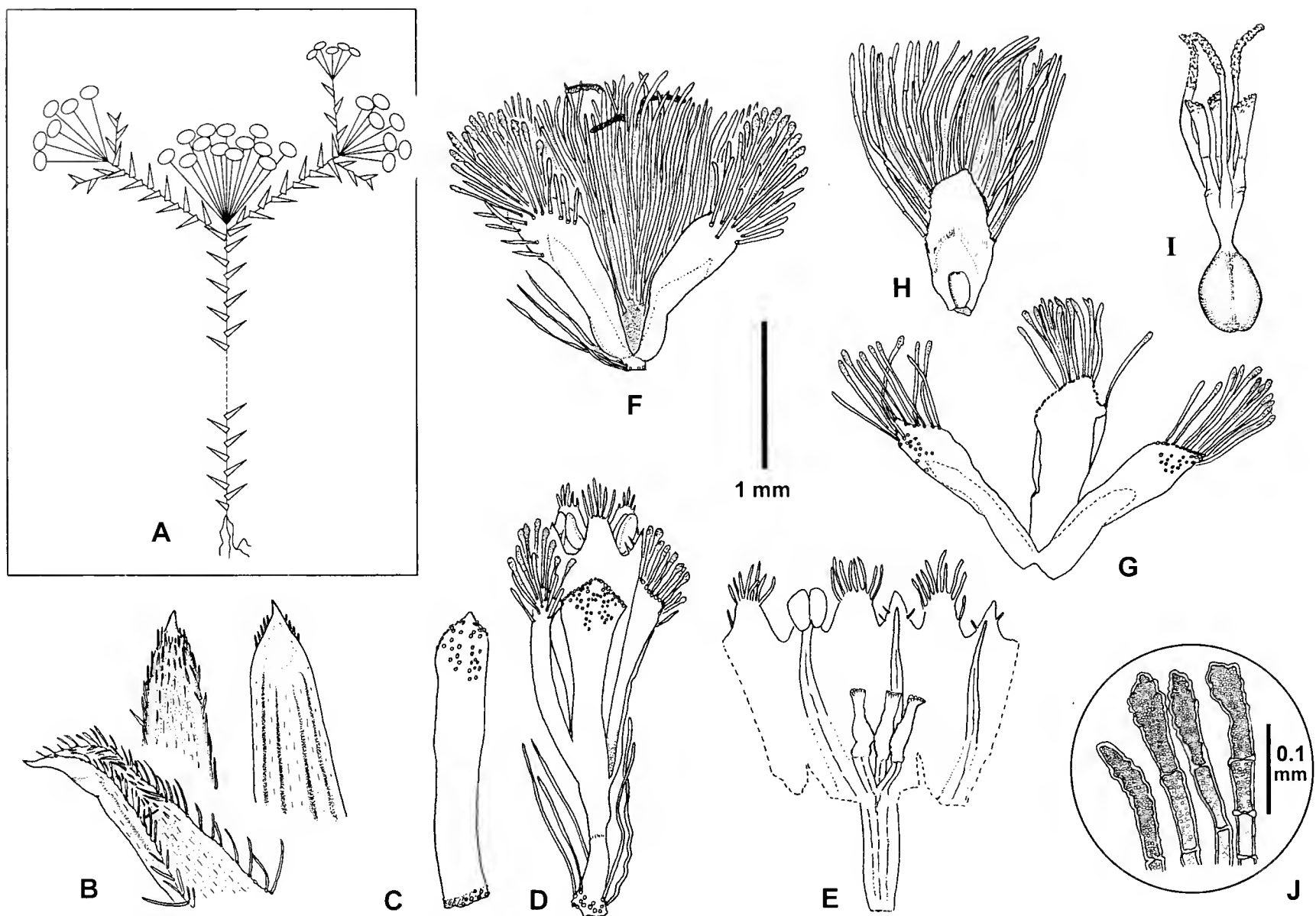


FIG. 5. *Paepalanthus piscatorum* habit, leaf detail, flowers. (A) Diagram of branching pattern. (B) Leaf tips, adaxial to left, abaxial to the right showing whitish tissue mass below epidermis. (C) Receptacular bract of staminate flower, abaxial, trichomes removed, basal cells remaining. (D) Staminate flower, trichomes removed from sepal in front. (E) Staminate corolla. (F) Pistillate flower. (G) Calyx after fruit dispersal. (H) Pistillate flower petal, adaxial surface, showing staminode. (I) Gynoecium. (J) Trichome tips of sepal apex. (B, van der Werff 15706; C–D, Vásquez 24602; E, Perea 3629; F–J, Weigend 98/498.)

0.25–0.5 mm long; appendage stalk 0.15–0.35 mm long; papillose portion narrowly infundibular, 0.35–0.65 mm long, in dry material commonly bright orange-red, or sometimes whitish except for dark red spot visible at base of papillose region, possibly colorless when fresh; the appendages half to slightly more than half the length of the styles, exsert from petal tips but remaining enclosed by the dense petal trichomes. Style branches 1.0–1.5 mm long, undivided, robust and persistent, surpassing the trichomes, the exsert tips decurved (or incurved after anthesis), papillose up to half their length, sometimes dark orange to red-brown, not retracted by corolla after anthesis. Gynoecium, like anthophore, microscopically glandular, the surface covered with tiny 1-celled globose brown trichomes. Only 2 developing seeds observed, still enclosed in fruit wall, ca. 0.6 mm long (Atkin 1).

ETYMOLOGY—The epithet *piscatorum*, Latin for “of the fishermen,” reflects the resemblance of the diaspore to a fishing fly (*mosca pesca*), as pointed out by contacts on social media.

PHENOLOGY AND REPRODUCTION—Collected in early flower in March and July, in full anthesis in June and August, and in late anthesis in September and October. Although the local climate is not strongly seasonal, this corresponds to the drier season of the year.

The material examined showed scarcely any evidence of seed set. Many ovaries had strongly concave locules suggesting ovule abortion. Only partially matured fruits were observed

(Atkin 1), and these were single-seeded by abortion and not yet dehiscent.

DISTRIBUTION AND HABITAT—*Paepalanthus piscatorum* is endemic to sandstone exposures of the eastern slope of the Andes in southern Ecuador (Zamora-Chinchipe) and northern Peru (Amazonas, Cajamarca, Loreto, San Martín). It occurs at elevations from 1200–2400 m in association with dense shrubby thickets and dwarf cloud forests, on ridgetops and plateau summits, in areas with frequent year-round fogs. Its long weak stems, unthickened at the base, may be partly supported by the dense vegetation, but it also may occur as an erect herb in open wet seepage areas and on *Sphagnum* mats. The lowest elevation records are those from 1200 m on ridgetops in the Cerro Tayu (Tayu Mujaji). Here it is cited by Vásquez et al. (2010, under “*Paepalanthus schomburgkii* Klotzsch ex Körn.”) as one of the dominant herbaceous species of sclerophyllous dwarf forest (*bosque enano* or “*uwejush*” in Aguaruna), the soil composed of a spongy humic layer over white sand. Its associates on these sites include species of Bromeliaceae and *Trichomanes* L. All other collections are from over 1800 m. It is recorded from “marshy areas, sometimes supported by vegetation” in the southern end of the Cordillera del Condor of Peru, and “on a sphagnum mat over bare sandstone” in the northern Condor (*P. piscatorum* var. *ecuadorensis*). In the vicinity of Abra Patricia, near the border of Amazonas and San Martín, it is reported from “montane

forest,” “*ceja de la montana*,” “*bosque enano de cumbres*,” and “*pajonal*” (Fig. 3).

CONSERVATION STATUS—Vulnerable, Criteria B1ab(iii). The species is known from at least eight localities, in a narrow altitudinal band ca. 430 km long and less than 15 km wide in the eastern Andes, with the extent of occurrence about 6450 km². Within this area, it is limited to small isolated wet microhabitats of ridges and seeps, on thin white-sand soils. The more isolated of these areas, due to their topography, and poor economic potential, may be relatively safe from disturbance. However, more accessible sites are vulnerable due to fragility of the thin soils, and may be subject to sand mining (Neill, 2007). In addition, the habitat itself may suffer from climatic drying. The lack of seed set observed in all mature specimens of both varieties is also cause for concern.

DISCUSSION—*Paepalanthus piscatorum* has a distinctive architecture, with long spindly primary stems topped by terminal fascicles of inflorescences, which in turn are closely flanked by 1–5 subterminal (acrotonous) fertile branches typically arranged in subopposite pairs. These branches in turn may produce additional fertile laterals, forming inflorescences of up to three orders of branching, the later formed fascicles composed of fewer capitula (Fig. 5A). While this branch architecture is common in the genus *Paepalanthus* (Stützel & Trovó, 2013), *P. piscatorum* is distinguished by its very long hollow stem, mostly unbranched except near the apex, the lack of a thickened or branched rhizome, and the sequence of subterminal flowering branches produced in relatively rapid succession. All these characteristics suggest the species is monocarpic. Hollow stems are rare in *Paepalanthus* (Sano, 1999) and probably suggest rapid growth.

Paepalanthus piscatorum was earlier mistaken for *P. schomburgkii* Klotzsch ex Körn. of Venezuela, by Vásquez et al. (2010) who cited it as an example of a floristic link between Venezuelan Guayana and the sandstone cordilleras of northern Peru. However, *P. piscatorum* is easily distinguished from this and other species of *P. subg. Monosperma* Hensold by its characteristic branching pattern as well as numerous floral characters. Its closest affinities appear to be with *P. intermedius* Körn. (syn.: *P. stuebelianus* Ruhland), a smaller, more densely branched plant commonly collected just to the south and at slightly higher elevations, in the Rio Utcubamba watershed in southern Amazonas (Fig. 3). *Paepalanthus intermedius* differs from *P. piscatorum* by producing only 1–2(–5) inflorescences per fascicle, and a more abundant, less symmetrical production of flowering branches per parent axis. In addition, the stems of *P. intermedius* are solid, frequently branched from the base and sprawling, while *P. piscatorum* develops weak basal branches only rarely.

However, the capitula and flowers of these two species are identical in most respects. In both species the corolla of the pistillate flower is densely and persistently plumose on the outer surface except for the glabrous base, which thickens and partially encloses the ovary with age (Fig. 4D). The corollas adhere to the fruit and are dispersed with it at maturity, whether or not seed set occurs. The trichomes of the corolla spread outwards when wet and probably aid in ejection of the diaspore from the capitulum (Fig. 4C, arrow). The staminate corollas of *P. piscatorum* differ from those of *P. intermedius* by the prominent secondary (interstaminal) lobes with ciliate margins. These are sometimes larger than the glabrous primary lobes opposite the staminal filaments (Fig. 5D,E). This character can be difficult to see since the secondary lobes become in-

volute, probably soon after anthesis, so that the trichomes fold into the corolla tube. Most species of *Paepalanthus*, including *P. intermedius*, have glabrous male corollas, the only recorded exceptions being *P. subg. Xeractis*, *P. trichopetalum* Körn., and a few other rosulate species of Minas Gerais, Brazil (Hensold 1988).

Also unusual in *P. piscatorum* is the red-orange color of the nectaries (appendages), observed in most but not all dried specimens, and not observed in *P. intermedius*. In some collections, including the type, the color is confined to a dark spot visible at the base of the papillose region of the nectary where the vascular bundles terminate. In most dried specimens, the entire papillose portion of the nectary is orange to scarlet, and darker streaks sometimes appear at the base within (Fig. 4E,F). However, one photo of a fresh inflorescence (*J. L. Clark 11797*) shows nectaries colorless at anthesis (AABP Atrium website; image *jlclark_011797_04*). Hansen et al. (2007), in a survey of angiosperms with colored nectar, found nectar color to vary between individuals grown under different conditions, possibly as a function of flower age or pollinator shortage; some nectars, such as those containing phenols, darken as they oxidize. Thus the colorless nectaries of some individuals of *P. piscatorum*, and perhaps of *P. intermedius* as well, may be due to a greater local abundance of pollinators removing the nectar, or to differences in microclimate affecting rate of evaporation.

Paepalanthus intermedius and *P. piscatorum* have a similar flowering season, but *P. intermedius* more frequently shows signs of seed set, with seeds 0.6–0.7 mm long, yellowish to red-brown, with short weak pseudotricones. Differences between the two species are summarized in the key in Section 3 below.

HYBRIDS—Until recently, the known distributions of *P. intermedius* and *P. piscatorum* were isolated by 50 km and the 3500-m ridge dividing the Utcubamba and Imaza watersheds. However, in 2009 a new road opened crossing the ridge, and two recent collections along this road just north of the ridge-line show some intermediacy and suggest interbreeding. The collection *van der Werff 25237* fits well within my concept of *P. intermedius*, except that the corolla lobes opposite the stamens are abnormally tufted at the abaxial apex, mimicking the sepal pubescence. Thus both the position and morphology of these trichomes differ from those of *P. piscatorum*. The ovaries of this collection are swollen with immature seeds. The other specimen, *van der Werff 25282*, more closely resembles *P. piscatorum* in the long stems and leaves, and in the terminal fascicle of nine robust inflorescences flanked by four fertile branches. However the stems are described as “creeping” with small weak vegetative branches emerging from several consecutive internodes halfway up. In addition the staminate corolla lobes are glabrous as in *P. intermedius*, and the gynoecea show unusual developmental irregularities in the nectaries and ovaries, such as aborted locule walls suggesting possible hybridization.

AFFINITIES—*Paepalanthus piscatorum* is provisionally placed with *P. intermedius* in *P. subsect. Polyactis*, a group found mostly in eastern Brazil, characterized by long aerial stems and branching just below the fertile shoot apex. However, the unusual floral and diaspore morphology of *P. piscatorum* and *P. intermedius* differs from all species of *P. subsect. Polyactis* I was able to examine, either directly or through published descriptions. Some species of *P. subsect. Polyactis* have corollas sparsely long-pilose on the outer

surface, but more have petals merely tufted at the apex, similar to *P. subsect. Dichocladus* (Fig. 1F,N). The species of *Paepalanthus* found most closely to match *P. piscatorum* and *P. intermedius* in floral morphology, including that of corolla, gynoeceum, and diaspore, is the eastern Brazilian species *P. distichophyllus* Mart., the sole representative of *Paepalanthus* sect. *Dyostiche* Ruhland. The petals of pistillate flowers of *P. distichophyllus* differ by the pubescence inserted on both surfaces, and the bases not thickening in fruit, but the distinct appearance of the diaspore is very similar. It should be noted here parenthetically that in his description of *P. sect. Dyostiche*, Ruhland (1903) misquotes Körnicke (1863) and erroneously describes the sepals, rather than petals, as pubescent on both surfaces. *Paepalanthus distichophyllus* was segregated into *P. sect. Dyostiche* by Ruhland due to its distichous, equitant leaves, but the general branching pattern, as analyzed by Stützel and Trovó (2013), is similar to *P. piscatorum*, as well as to other members of *P. subsect. Polyactis*. Unlike *P. piscatorum*, however, *P. distichophyllus* branches from the base from a short woody rhizome, and the aerial stems are solid within (vouchers: Mello Barreto 8546, 9892 at F). In recent molecular studies of Brazilian species, *P. subsect. Polyactis* has emerged as deeply polyphyletic (Andrade et al., 2010; Trovó et al., 2013). One representative of *P. subsect. Polyactis*, *Paepalanthus stannardii* Giul. & L. R. Parra, emerged as sister to *P. distichophyllus* (Trovó et al., 2013), but I was unable to examine the flowers of this species.

The pistillate corollas of the cushion plant *Paepalanthus dendroides* (Kunth) Kunth, in *P. subsect. Cryptanthella*, approach those of *P. piscatorum* in morphology but the pubescence is not as dense, occurs on both surfaces, and the petal trichomes are finer and tuberculate (Hensold, 2016).

Key to the Varieties of *Paepalanthus piscatorum*

- 1 Stems 2–3 mm in diameter; leaves up to 4.5 cm × 5.5 mm; inflorescences up to 30 per node; staminate flowers at least 50% more numerous than pistillate flowers; pistillate flowers with sepals ca. 3 times longer than wide; ovaries up to 0.55 mm long *P. piscatorum* var. *piscatorum*
- 2 Stems 5–6 mm in diameter; leaves ca 6 cm × 10 mm; inflorescences more than 50 per node; staminate flowers about equalling pistillate flowers in number; pistillate flowers with sepals ca. twice as long as wide; ovaries more than 0.6 mm long *P. piscatorum* var. *ecuadorensis*

Paepalanthus piscatorum var. *piscatorum*

Figures 3, 4A–D, 4F, 5

Stems up to 1.6 m long, 2–3 mm in diameter. Leaf lamina 1.7–4.5 cm long, and 3–5.5 mm wide at base, often conspicuously long-ciliate at base only, margins glabrous above or the cilia sometimes extending to apex and progressively shorter above, or short-ciliate, mixed with long cilia all the way to apex, the cilia antrorse-appressed near apex. Inflorescences in clusters of 5–30; capitula 4–5.5 (–6) mm in diameter. Involucral bracts cuspidate to aristate; floral bracts ca. 0.15 mm wide, linear-subspatulate. Floral trichomes (at apex of floral bracts and sepals) usually weakly tuberculate in outline. Ratio of staminate to pistillate flowers per capitulum ca 1.7–2.7 (4 capitula counted), both sexes found in outer whorl of capitulum. Staminate flowers with pedicels 0.2–0.5 mm long, sepals 1.0–

1.7 mm long × 0.3–0.5 mm wide, anthophore 0.4–1.0 mm long, tube 0.7–1.5 mm long. Female flowers with pedicels 0.03–0.13 (–0.33) mm; sepals 1.1–1.5 × 0.35–0.5 mm, [l:w 3:1], sepal trichome tuft 0.5–0.75 mm long, petals (0.85–) 1.2–1.5 × 0.35–0.5 mm, the whole corolla with trichomes (1.7–) 1.8–2.0 mm long. Ovary 0.45–0.55 mm long, style column 0.35–0.5 mm long, appendages with stalk 0.15–0.35 mm long and papillose portion 0.35–0.55 mm long.

DISTRIBUTION AND HABITAT—Northern Peru (Amazonas, Cajamarca, Loreto, San Martín), at 1200–2400 m. For habitat, see species discussion.

CONSERVATION STATUS—VU B1ab(iii). This variety is known from seven recent collections in a narrow strip ca. 250 km long by 15 km wide, with known extent of occurrence of about 3750 km².

PARATYPES—PERU. Cajamarca: Prov. San Ignacio, vicinity San José de Lourdes, 05°02'S, 78°51'W, ca. 1900–2200 m, June 1975 [anthesis and young seed], *David Atkin 1* [Princeton avifaunal survey, led by J.W. Fitzpatrick] (F); Prov. San Ignacio, Distrito Huarango, Poblado Selva Andina, 05°03'50"S, 78°43'19"W, 2378 m, 21 Aug 2007 [anthesis], *J. Perea et al.* 3629 (F, MO). Amazonas: Prov. Bongará, Ingenio [Pedro Ruiz]–Rioja road, 'Rio Nieve,' 2000 m, 10 Aug 1983, *W. Rauh* 63752 (USM); Prov. Bagua, Dist. Imaza, Quebrada Almendra, Cerro Tayu, 05°15'56"S, 78°22'07"W, 1200 m, 20 Jul 2004 [bud], *R. Rojas et al.* 3171 (F, MO); Prov. Bagua, Dtto. Imaza, Tayu Mujaji, comunidad de Wawas, 05°15'56"S, 78°22'07"W, 1200 m, 21 Oct 1997 [late anthesis], *R. Vásquez et al.* 24602 (F, MO, USM); Prov. Bongará, close to the border with San Martín, along road from Pedro Ruiz, past Laguna de Pomacocha to Rioja, 05°41'S, 77°48'W, 1950 m, 4 March 2001 [bud], *H. van der Werff et al.* 16719 (F, MO). San Martín: Prov. Rioja, Bosque Protección Alto Mayo, Trocha Las Palmas, near Venceremos, Km 382.5 on Hwy 5N, 05°38'41"S, 77°44'34"W, 1800–2200 m, 4 Jun 2010 [anthesis], *J. L. Clark et al.* 11797 (NY photo); Prov. Rioja, Pedro Ruiz–Moyobamba Road, km 368, Campamento García, 05°45'S, 77°43'W, 2200 m, 14 Aug 1983 [anthesis], *D.N. Smith* 4822 (MO, USM); Prov. Rioja, along road Rioja–Pedro Ruiz, El Mirador, 05°40'29"S, 77°46'25"W, 1850 m, 25 March 1998, [capitulum expanded, fls in bud], *H. van der Werff et al.* 15706 (F, MO, USM). Loreto: Prov. Amazonas, Distr. Balsapuerto, Cordillera Escalera, Campamento Cumbre–Alto Cachiyacu, 5°52'2.1"S, 76°46'29.3"W, 1930 m, 22–24 Sept 2013, *M. Rios et al.* 3303 (AMAZ [photo]).

Paepalanthus piscatorum var. *ecuadorensis* Hensold, var. nov.

Figures 3, 4E

TYPE—Ecuador. Zamora-Chinchipe: El Pangui, Cordillera del Cóndor. Summit of sandstone plateau of Cordillera, SE headwaters of Río Wawaime, near western edge of undulating plateau, above proposed Ecuacoriente copper mine area, [ca. 03°35'20"S, 78°24'29"W], 1930 m, 19 Sep 2006, *D. Neill & W. Quizhpe* 15235 (holotype, F; isotypes, BOCH n.v., HUT n.v., LOJA n.v., MO, QCNE n.v.).

DIAGNOSIS—See key above.

DESCRIPTION—Stems at least 20 cm long (base not seen), 5–6 mm in diameter, lateral branches initiated at base of inflorescence but not well-developed in the single specimen observed. Leaf lamina ca. 6 cm long and 1 cm wide at base, densely short-ciliate along margin, not long-ciliate at base. Inflorescences

in terminal clusters of up to 78; capitula 5–6 mm in diameter; involucre bracts cuspidate. Floral bracts 0.3–0.7 mm wide, oblong-subspatulate. Floral trichomes (at apex of floral bracts and sepals) smooth in outline, not tuberculate. Ratio of staminate to pistillate flowers ca. 1:1 (1 capitulum counted), mostly pistillate flowers found in outer whorl of capitulum. Staminate flowers with pedicels 0.5–0.6 mm long; sepals 1.25–1.4 mm long, 0.55–0.65 mm wide; anthophore 0.55–0.85 mm long; tube 0.95–1.15 mm long. Female flowers with pedicels 0.2–0.3 mm, sepals 1.35 mm long, 0.7–0.8 mm wide [l:w about 2:1 or less], sepal trichome tuft 0.4–0.65 mm long, petals 1.2–1.6 × 0.4–0.6 mm, (petals probably normally free and basally thickened as in the typical variety, but in the single specimen observed petals often irregularly fused at the margins and thickening of both calyx and corolla may be irregular or lacking), the whole corolla including trichomes 1.85–2.35 mm long. Ovary 0.65–0.75 mm long, style column 0.25–0.35 mm long, appendages with stalk 0.2–0.25 mm long and papillose portion 0.45–0.65 mm long.

DISTRIBUTION AND HABITAT—Known only from the type, growing near the border with Peru, on an “exposed bare sandstone outcrop amid carpet of *Sphagnum* moss,” in an area of dense dwarf forest, at 1930 m.

CONSERVATION STATUS—Endangered, B1ab(iii). The only specimen of this variety was collected on a sandstone tepui summit above the Ecuacoriente copper mine. The summit area is designated for preservation (Neill et al., 2007).

DISCUSSION—This monotypic variety is found at a single site 165 km distant from the northernmost specimens of the type variety, and is much more robust, its leaves and floral parts all proportionately broader. It also has slight abnormalities in the development of the flowers. It is recognized as a variety with some hesitation, as it may prove to be merely an extreme form in a continuously varying species.

The collector described the plant as a “rosette-herb,” in reference to a common growth form of the high Andes, in which the stem is narrow and erect with green leaves clustered in a rosette towards the apex, and the lower leaves senescent. Basal rosettes were not observed (Neill, pers. comm.).

***Paepalanthus* subg. *Platycaulon* Körn.,
Fl. Bras. 3(1): 394. 1863**

The authorship of *P.* subg. *Platycaulon* is often attributed to Martius (1834, 1835). However, his proposal of this and three other groups (*Brachycaulon*, *Eustelechon*, and *Xeractis*) into which “each of the three genera [*Eriocaulon*, *Nasymthia* and *Paepalanthus*] are to be divided” is not considered valid publication (Kanchi Gandhi, pers. comm.). The subgenus was first validly published by Körnicke and later divided by Ruhland (1903) into two groups treated informally as sections by recent authors (e.g., Tissot-Squalli, 1997c; Andrade et al., 2010), but without the basionym citation required by the International Code of Nomenclature (Melbourne Code), Art. 41.5 (McNeill et al., 2012).

***Paepalanthus* [subg. *Platycaulon*] sect. *Conferti* (Ruhland)
Tissot-Squalli ex Hensold, stat. nov.**

Paepalanthus [infragen. unranked] *Conferti* Ruhland, Pflanzenr. IV. 30: 201. 1903.

***Paepalanthus* [subg. *Platycaulon*] sect. *Divisi* (Ruhland)
Tissot-Squalli ex Hensold, stat. nov.**

Paepalanthus [infragen. unranked] *Divisi* Ruhland, Pflanzenr. IV. 30: 201. 1903.

***Syngonanthus* Ruhland**

***Syngonanthus peruvianus* Ruhland,
Pflanzenr. IV. 30: 253. 1903**

Figures 6, 7

TYPE—Peru. Amazonas: “Cuesta de Lejía cerca de Molinobamba,” [*sphalm.* “Moyobamba” in protologue], 4 Jun 1875, A. Stübel 19b. (Lectotype, designated by Watanabe et al. 2015a: B [100250262]; isolectotype B [100250264]).

Syngonanthus yacuambensis Moldenke (1953: 182). **TYPE**: Ecuador. Azuay—Oriente border: between Oña and the río Yacuambi, Eastern Cordillera, 10–19 Sept 1945, Francisco Prieto P-197 (Holotype: NY; isotypes: F!, G, GH, MO!, P, US). (Synonymy *fide* Watanabe et al. 2015a)

DESCRIPTION—Plants perennial, varying in *habit* from acaulescent rosettes to clumps, mats, or lax cushions up to 20 cm in diameter, with erect branches up to 8 cm long. Stems leafy, pale with a thin-walled epidermis, except for the prominent rigid leaf scars, the cortex spongy (aerenchymatous) to somewhat fibrous, the whole stem often sheathed by the descending spongy white adventitious roots cohering to its surface. *Leaves* narrowly linear-acicular to filiform to linear-lanceolate, chartaceous, 1–5 cm long, 0.5–4 mm wide, (1–)3–11-nerved, white-costate abaxially; leaf apex subacute to short acuminate, often slightly canaliculate-recurved in younger leaves, probably hydathodal, in older leaves becoming callose-thickened, minutely retuse, bilobed or praemorse, pitted at the apical margin, or (in plants of Azuay, Ecuador) short-acuminate and minutely pitted adaxially just below the apex; leaf pubescence of appressed roughened malpighian hairs, thicker on adaxial surface, or (in plants of Amazonas, Peru) grading into erect basally attached 1-celled hairs of about the same size and the upper surface densely hirsutulous when young; mature leaves often early glabrate except for the woolly bases. *Inflorescences* borne in clusters of 1–11, very often but perhaps not always on distinct leafless, villous short shoots with an involucre of bracts at the apex; the short shoots nearly obsolete to up to 10 mm long and hidden by the leaves, rarely up to 20 mm long and exsert (*Smith 4150*); inner bracts of the involucre up to 15 mm long, the outer shorter, all similar to reduced foliage leaves but often with some gland-tipped hairs. *Peduncles* at flowering or fruiting 4–30 cm long, probably longer in fruit than at anthesis, often at different flowering stages within a cluster; peduncle sheaths 1.0–4.5 cm, the open apex 2.2–9 mm long, acute to acuminate at tip, the sinus usually broadly rounded, sometimes acute; peduncles 3–6-costate, the sheaths and peduncles pubescent with a mixture of malpighian and filamentous hairs, sometimes also with capitate-glandular filamentous hairs, pubescence often densely sericeous at peduncle apex. *Capitula* 6–8(–10) mm in diameter, whitish, obconic, becoming globose with age. Involucre bracts cream-white, oblong-obovate, convex-acute, glabrous or sparsely and inconspicuously appressed-pilose on dorsum, in ca. 3–4 series, subequaling to equaling the flowers, reflexed and hidden in mature globose capitula. Receptacle densely pilose. Receptacular bracts absent. *Staminate flowers*: Pedicels 0.6–0.9 mm long. Sepals white, 1.5–2.4(–2.8) mm long, obovate, acute to apiculate, fused basally ca. 1/4–1/3 of their length, the lobes

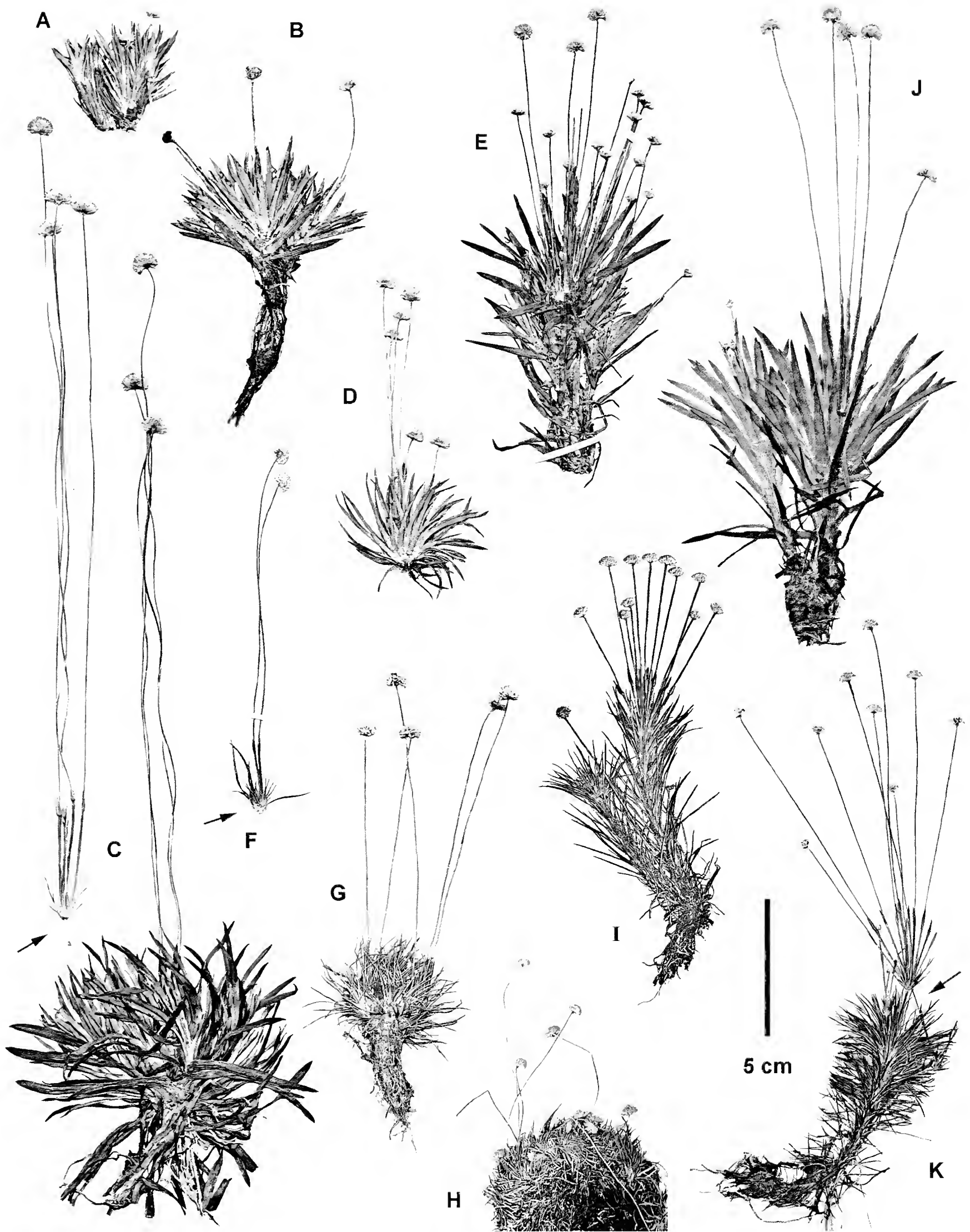


FIG. 6. Variation in *Syngonanthus peruvianus*. (A–B). Ecuador, Azuay. (C) Peru, Cajamarca, Prov. Cutervo. (D–E) Amazonas, Prov. Leimebamba. (F–I) Amazonas, Prov. Chachapoyas, vicinity of Molinopampa. (J–K) Pasco, Prov. Oxapampa. Arrows indicate flowering axes. (A, Holm-Nielsen 4814; B, Holm-Nielsen 5080; C, Sanchez 6268; D, Hutchison 5556; E, Quipuscoa 1361; F, Stübel 19b; G, Wurdack 1379; H, Pennell 15769; I, Bussman 17174; J, Vásquez 30315; K, Smith 4150.)

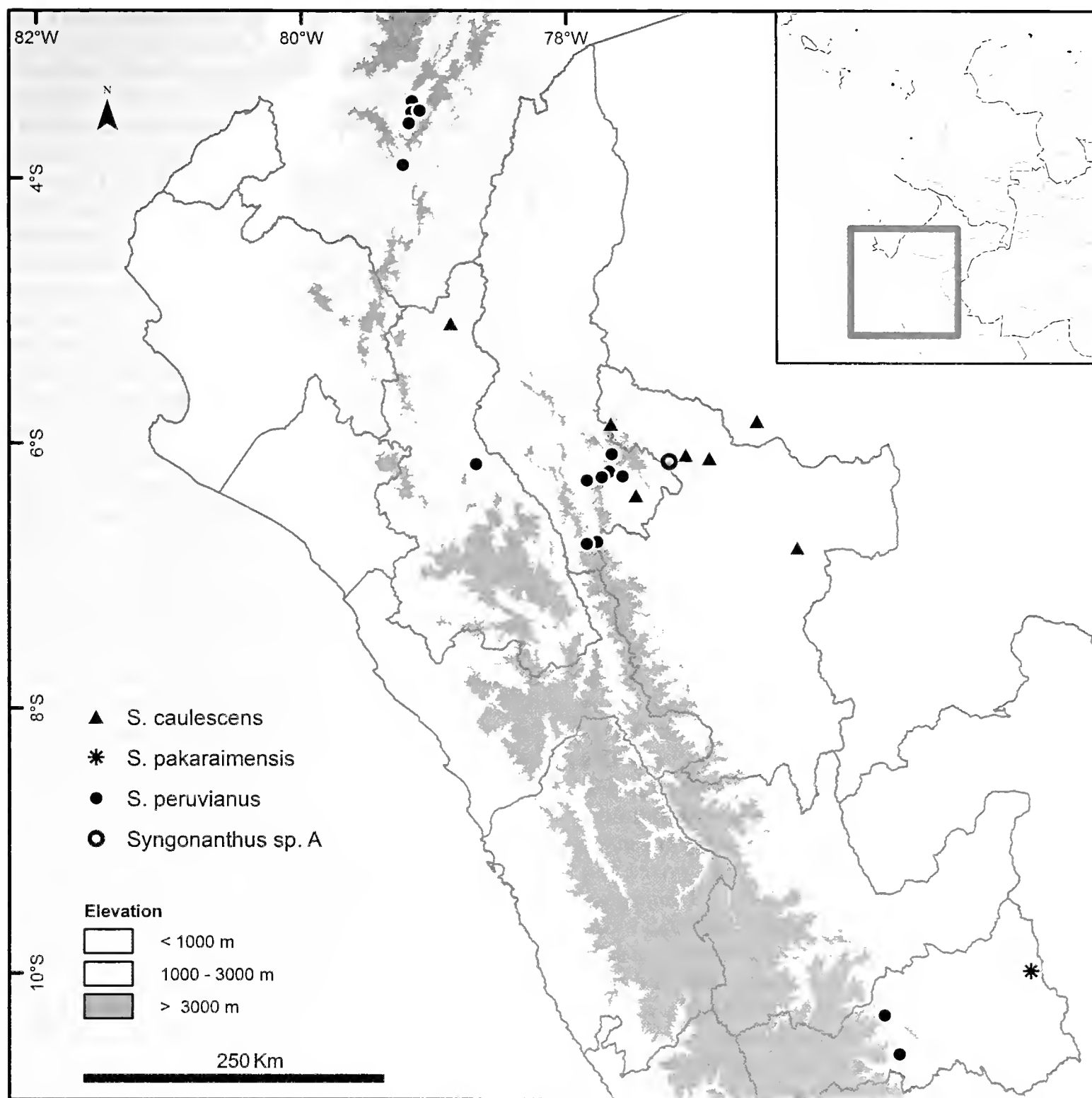


FIG. 7. Distribution of *Syngonanthus* species in montane Peru, above 1000 m. The distribution of *S. caulescens* in the Amazonian lowlands is not shown.

navicular, white, bearded on the inner surface with straight white trichomes, sometimes also on the outer dorsum below the apex, the apex itself glabrous; corolla membranous, glabrous, the narrow anthophore less than half the corolla length, the lobes subacute, involute after anthesis; stamens with filaments fused to base of corolla, about equalling the corolla lobes or slightly exsert; anthers ca 0.3–0.4 mm; pistillodes present, clavate. *Pistillate flowers*: Pedicels 0.2–0.7 mm long. Sepals white, 1.9–2.7(–3.1) mm long, elliptic to obovate, navicular, sharply short-acuminate, glabrous or sparsely bearded at the middle on the inner surface; floral axis between sepals and petals glabrous; petals membranous to slightly thickened, broadly oblanceolate or elliptic, acute, shorter than sepals, the margins fused toward apex, free at base, sparsely to moderately long pilose externally near the middle or below, the upper fused portion of petals usually glabrous, the tips involute after anthesis; a minute staminodial scale present on inner petal base. Gynoecium with short style-column, the nec-

taries pale, prominent, clavate-infundibular, obscurely papillose, well-included in corolla at anthesis; stigmas simple. Seeds dark red-brown, ellipsoidal, 0.55–0.7 mm long, with rows of whitish, hygroscopic but somewhat weak pseudotrachomes.

PHENOLOGY—Collected in anthesis from late May to October, with peak flowering probably June to August. Also collected in senescent condition from March to early May and in November.

HABITAT AND DISTRIBUTION—Ecuador (Azuay, Loja); Peru (Cajamarca, Amazonas, Pasco), at 1850–3200 m, extending 950 km along the Andes (Fig. 7). In Ecuador it is known only from the vicinity of the Pan-American Highway from near Oña (Azuay) to just north of the city of Loja. It is not recorded from Podocarpus National Park where other Eriocaulaceae are abundant. In Peru, it is known from a few sites in the Amotape-Huancabamba zone (Cajamarca and southern Amazonas), and also in Oxapampa province in Pasco. It is recorded from seepage areas, flush bogs, old lakebeds,

Sphagnum mats, and on sandy streambanks, and may be partially submerged. It may occur on otherwise dry scrubby sites (Ecuador), in cloud forest (Peru), and in disturbed pasture and roadsides (Fig. 7).

DISCUSSION—Ruhland's concept of *S. peruvianus*, based only on the type, was of a rosette plant with the main axis apparently (“*primo intuito*”) fertile; that is, directly producing inflorescences. This would distinguish it from those species of *Syngonanthus*, once placed in *Paepalanthus* subg. *Andraspidopsis* Körn. (1863), in which inflorescences are borne apically on long naked “fertile” axes arising from a primary “sterile” rosette. These are termed “synflorescences” by Echternacht et al. (2014). In fact, close examination shows that most specimens of *S. peruvianus* bear inflorescences on short modified naked branches that are difficult to detect among the leaves. (Examples are indicated by arrows in Figs. 6C,K.) In some cases the fertile axis is nearly obsolete, but the “involucel” or apical whorl of reduced leaves investing the peduncles can be seen (Fig. 6F). It is difficult to confirm the presence of this character in dried material without damaging the specimen. However in some individuals (e.g., in *Quipuscoa* 1361, Fig. 6E), I could not detect either an elongated axis or an involucel; the leaves directly below the peduncles seemed undifferentiated from normal foliage leaves. Ruhland (1903, pp. 28–29) described his surprise at making a similar discovery about *Syngonanthus fischerianus* (Bong.) Ruhland, in which short naked fertile axes are sometimes, but not always, distinguishable, and were entirely missed by Körnicke (1863). For this reason Ruhland rejected the taxonomic distinction between *Paepalanthus* subg. *Psilocephalus* Körn. (1863), with inflorescences borne on the main stem, and *P.* subg. *Andraspidopsis*, with inflorescences borne on modified secondary axes, and merged these two groups into *Syngonanthus* sect. *Dimorphocaulon* Ruhland (= *Syngonanthus* sect. *Syngonanthus*).

Ruhland characterized the habit of *S. peruvianus* as a simple or clumped rosette, with leaves 1 mm wide covered with “dense long hairs,” and capitula bright yellow. He considered *S. peruvianus* distinguishable from *Syngonanthus nitens* (Bong.) Ruhland mainly by the hairy leaves, and later identified a glabrate-leaved specimen from the same locality (Weberbauer 4328) as *S. nitens*. In fact, *S. peruvianus* only rarely has markedly pubescent leaves, and these only when young. The pubescence of the lamina is usually of flattened malpighian hairs, single-celled (above the basal and collar cells) with a whitish, roughened epidermis, but these malpighian hairs may intergrade with basally attached trichomes, which are similar in appearance and usually early deciduous. It lacks the long, fine, multicellular filamentous hairs found in *Syngonanthus pakaraimensis* Moldenke and “*Syngonanthus* sp. A” of Peru (see key below). The yellow capitulum color observed by Ruhland was probably an artefact of preservation or mounting, as collectors consistently describe the capitula as white. Pink-stained capitula have also been observed.

Peduncle length, leaf width, and stem elongation vary considerably, such that extreme variants are not easily recognized as the same taxon. Peduncle length is widely variable within populations and even individuals, and suggests continued elongation of peduncles after anthesis, recently observed in other Eriocaulaceae (Hensold et al., 2012; Hensold, 2016). Variation in leaf width and stem length, on the other hand, may be partly geographic. Specimens from Ecuador (“*S. yacuambensis*”; Figs. 6A,B) and Cajamarca, Peru, usually exhibit a broad-leaved rosette or short-caulescent habit. The Cajamarca

(Cutervo) specimen (Fig. 6C) is the largest of any seen, as to leaf length and width, capitulum diameter (to 10 mm, versus 6–8 mm), and even flower size (sepals of staminate and pistillate flowers 2.4–2.8 mm and 2.7–3.1 mm, respectively, versus 1.5–2.4 mm and 1.9–2.7 mm in other specimens). In Amazonas Department, specimens from the vicinity of Molinopampa and east along the Rio Ventilla watershed (Figs. 6F–I) tend to have narrower leaves and a stronger tendency to stem elongation and perhaps mat formation than material from elsewhere in Amazonas (Figs. 6D–E), but the range of variation overlaps, preventing recognition of distinct varieties. In Pasco, caulescent plants with both wide (Fig. 6J) and very narrow, almost needle-like, leaves (Fig. 6K) are known, separated by only 35 km. Of these, the latter narrow-leaved plant (*D. N. Smith* 4150; Fig. 6K), represents the southernmost and lowest elevation recorded for the species, and until recently had seemed to me and other specialists in the family to be a distinctive undescribed species, but given similar collections now known from Molinopampa, this now seems unlikely. It may be noted that seemingly discontinuous, polymorphic variation in leaf width occurs in other species of Eriocaulaceae, for example, the complexes surrounding *Rondonanthus aco-panensis* (Moldenke) Hensold & Giul. (Hensold & Giulietti, 1991), *Paepalanthus elongatus* (Bong.) Körn., *S. simplex* (Miq.) Ruhland (unpublished observations), and *S. nitens* (Watanabe, 2009). Variation in leaf width may also be environmental, perhaps light-dependent. The degree of stem elongation may be influenced by substrate, such as occurrence in thick *Sphagnum* mats.

Some individuals of *S. peruvianus* may be difficult to distinguish from *Syngonanthus caulescens* (Poir.) Ruhland, since both species show broad variation in habit. However *S. caulescens* is normally a caulescent unbranched annual which doesn't form mats, and *S. peruvianus* forms clumps or mats, with stems regularly branching below the inflorescence. When not distinguishable by habit, the two can be distinguished by capitulum size, floral characters, and seed size (See Key, Leads 10 and 12). Though *S. caulescens* has been collected in close proximity to *S. peruvianus* in Peru, it is not strictly sympatric, and is not known above 2000 m. The affinity of the two species is supported by molecular data (Watanabe, 2015; Watanabe et al., 2015b), suggesting placement of *S. peruvianus* in *Syngonanthus* sect. *Carphocephalus* (Körn.) Ruhland rather than in *S.* sect. *Syngonanthus*, as treated by Ruhland (1903).

PART 2. A REVISED CHECKLIST OF THE ERIOCAULACEAE OF PERU

Overview

The *Catalogue of the Flowering Plants and Gymnosperms of Peru* (Brako & Hensold, 1993) and published updates (Vásquez & Rodríguez, 2002; Ulloa Ulloa et al., 2004) present five genera and 22 species of Eriocaulaceae in Peru, including four endemic species and one endemic variety. This new update is based on observations of 302 specimens as well as records cited in recent literature (Tissot-Squalli, 1997a,b; Watanabe et al., 2015a,b; Hensold, 2016). It includes a total of 31 species, one with two varieties in Peru, representing the addition of 12 new species records and one new variety record, the elimination of three species from the list, and one tagged as doubtful; three name changes due to synonymy; and

19 additions or deletions of regional (departmental) distribution records. One species on the list (*Syngonanthus* sp. A) is of uncertain taxonomic status and still unnamed, but definitely distinct from other Peruvian taxa. Specimen determinations were confirmed by the author, except for *Paepalanthus* subg. *Platycaulon* (taxa 7, 9, 15–17, 20), which needs further taxonomic attention.

The number of endemic taxa has doubled, with a total of eight endemic species and two endemic varieties. The assessments of conservation status by Monsalve and León (2006) are updated as necessary, and provisional assessments proposed for all endemics except *Paepalanthus crassicaulis* Körn. and *Paepalanthus longivaginatus* Tissot-Squalli (*P.* subg. *Platycaulon*), due to my lack of familiarity with this subgenus. Conservation status of endemics is assessed according to the IUCN Guidelines and Criteria (IUCN 2014). The endemic taxa in the numbered list are 2, 7, 10–13, 15, 18a, 19, 21.

Sample photos of all species are provided in a supplementary PDF file available online (<http://fieldmuseum.org/fieldiana-hensold>).

Comments on Distribution Patterns

In Peru, Eriocaulaceae occur principally on Amazonian white sands, and in wet montane forest and páramo of the sandstone-rich Eastern Cordillera. Only in the Amotape-Huancabamba zone in northern Peru do a few species cross to the Central and Western Cordilleras. Eight species, none of which are endemic, occur exclusively at or below 1000 m in eastern Peru. Five of these are thus far recorded in Peru only at Pampas del Heath in Department Madre de Dios on the Bolivian border, including four outliers of Brazilian and Bolivian savanna (*cerrado*) species. Six species of páramo cushion plants occur exclusively at 2700–4000 m. The remaining species are found in montane forest openings, cloud forest or shrublands at about 1200–3200 m. The common widespread annual species *S. caulescens* (Poir.) Ruhland has the widest elevational distribution of any Peruvian eriocaul, from the Amazon Basin at 200 m to 2000 m in San Ignacio province, Cajamarca.

Both overall diversity and occurrence of endemic taxa is greatest in montane northern Peru, in the departments of Amazonas, Cajamarca, Lambayeque, Piura, and San Martín north of 7°40'S latitude. This region, together with parts of southern Ecuador, comprises the phytogeographically significant Amotape-Huancabamba zone, a low depression in the Andes of much-dissected topography (Weigend, 2002). Of the 19 species and one variety recorded here, seven species are endemic to this region, and *P. piscatorum* is nearly so. In addition, two Andean cushion plants, *Paepalanthus lodiculoides* Moldenke and *P. pilosus*, find their southern terminus in this zone, where the typical wet páramo formations of the north Andes terminate and give way to the drier jalca and puna formations of the south (Luteyn, 1999). In the eastern Cordillera south of the Amotape-Huancabamba zone, 11 species are found, including five species shared with northern Peru, and two narrowly restricted endemics.

Paepalanthus subg. *Platycaulon* (1863) includes some of the most conspicuous and commonly collected species of the montane forest zone, but most of the 84 specimens observed have not been reliably identified to species. All Andean species belong to *Paepalanthus* sect. *Conferti*, a group

also well-represented in the Atlantic Forest zone of Brazil. Members of this group have been recorded from Amazonas, Cajamarca, Huánuco, Junín, and Pasco at 1950–3200 m. They are reported from montane forest openings, dwarf sclerophyllous forest on sandstone ridges, secondary scrub (*matorral*), rocky slopes, wet mossy sites, and disturbed or burned areas. In southern Ecuador one species has been reported as an important pioneer of landslide-denuded areas (Lozano et al. 2008).

Neill (2007), Vásquez et al. (2010) and others have recently discussed links between the sandstone cordilleras of eastern Peru and the Guiana Highlands of northern South America. While some records (*P. dichotomus* subg. *glabrescens* and *P. schomburgkii* sensu Vásquez 2010) have been reinterpreted taxonomically in this paper and no longer provide such evidence, there are four Peruvian species, including three of the new records, which are disjunct between Peru and the Rio Negro basin or Guiana Highlands. *Syngonanthus trichophyllus* Moldenke in Loreto is found at least 650 km from the nearest neighboring population in the Rio Apaporis basin in Vaupés, Colombia. *Syngonanthus* sp. A, of Rioja Province in San Martín, is also disjunct by about 1000 km from its nearest relations along the Rio Apaporis. *Paepalanthus bifidus* (Schrad.) Kunth, also collected near Rioja, is disjunct by nearly 2000 km from the closest known populations on sand *campina* in Manaus, Brazil. The record of *Syngonanthus pakaraimensis* Moldenke var. *pakaraimensis* from the Cerro del Sira (see Fig. 7) is the most surprising. This robust perennial is the only strictly upland species of these four, and is disjunct 2000 km from its main distributional range among the sandstone tepuis of Venezuela and Guyana.

Taxa Listed by Region

Taxon numbers correspond to the list below. Peruvian endemics are in **boldface**.

The regional abbreviations follow usage of Brako and Zarucchi (1993).

AM – Amazonas: 2 – 4 – 7 – **10** – **11** – **13** – 16 – 18b – **19** – 23 – 28
 CA – Cajamarca: 1 – 2 – 8 – **10** – 18b – **19** – 20? – 23 – **28**
 CU – Cuzco: 6 – 8
 HU – Huánuco: 1 – 9 – **15** – 20?
 JU – Junín: 1? – 6 – 8 – 17?
 LA – Lambayeque: 18b
 LO – Loreto: **19** – 23 – 29 – 31
 MD – Madre de Dios: 3 – 22 – 23 – 24 – 25 – 26
 PA – Pasco: 14 – 6 – 8 – 17 – 27 – 28
 PI – Piura: **12** – 14 – 18b
 PU – Puno: 4 – 8 – **21**
 SM – San Martín: 1 – 5 – 9 – **18a** – **19** – 23 – 30 – 31

Taxa Listed by Elevation Range in Peru

The abbreviation “PL” refers collectively to the species of *Paepalanthus* subg. *Platycaulon*.

0–1000 m: 3 – 5 – 22 – 23 – 24 – 25 – 26 – 30 – 31
 1000–1800 m: 4 – 19 – 23 – 29
 1800–2600 m: 2 – 4 – 8 – 10 – 11 – 13 – 19 – 21 – 23 – 27 – 28 – PL

2600–3200 m: 1 – 2 – 6 – 8 – 11 – 12 – 13 – 18b – 28 – PL
3200–4000 m: 1 – 6 – 8 – 14 – 18a – 18b

Key to Symbols in Checklist

- * = New species or departmental record
- (^) = Name change
- [–] = Locality record deleted, based on misidentification or locality error
- [?] = Questionable record

Cited references are supplementary to those cited by Brako and Hensold (1993). For taxa with revised departmental distributions, all confirmed departmental records are listed. Information unchanged from the *Catalogue* is otherwise not repeated here. Vouchers are listed only for new country and department records not otherwise cited in the referenced literature. Species with names and distributions unchanged from the *Catalogue* are 4, 5, 9, 10, 21, 25, and 31.

Species Checklist

1. *Eriocaulon microcephalum* Kunth, Nov. Gen. Sp. (quarto ed.) 1: 253. 1815 [1816].

Eriocaulon brachypus van Heurck & Müll. Arg., Observ. Bot. 1: 96. 1870, non *E. brachypus* Bongard, 1831.

REGIONS— CA [–CU] HU JU[?] *PA SM

VOUCHER—Pasco, R. Vásquez 29031 (F, MO)

HABITAT—Boggy or partly inundated meadows in páramo, margins of montane forest and pajonal; 2700–3500 m.

DISTRIBUTION—From the Cordillera Central of Colombia south to Pasco, Peru; disjunct in the volcanic belt of central Mexico.

NOTES—The record from Cuzco was based on misidentified material of *Paepalanthus caryonauta* Hensold (*F. Pennell* 13864) cited in the *Flora of Peru* (Macbride, 1936). The record from Junín (*Weberbauer* 2269) cited in the same source has not been confirmed. The type of *E. brachypus* van Heurck & Müll. Arg. is *Spruce* 5862, cited erroneously in the protologue as from the Andes of eastern Peru. According to *Spruce's* field-books, the specimen is from “Condorasto,” in eastern Chimborazo, Ecuador.

2. *Eriocaulon peruvianum* Ruhland, Pflanzenr. IV. 30: 58. 1903.

REGIONS— AM CA*

VOUCHER—Cajamarca, S. Leiva et al. 1370 (F)

HABITAT—Seeps, ponds, swampy places in areas of montane forest; 2300–2860 m.

DISTRIBUTION—Classified as endemic, but similar to some Brazilian species and in need of taxonomic attention.

CONSERVATION STATUS—Vulnerable, Criteria B1ab(iii). This species is now known from five recent specimens and localities with an extent of occurrence about 150 km long and 30 km wide (ca. 4500 km²), growing in seepage areas, ponds and wet depressions, in grassland, pasture, montane forest, and along a roadside. Though it might be classified as Endangered, the recency and habitat data of collections suggests tolerance of disturbance. Not evaluated by Monsalve and León (2006), who were only aware of the type collection.

3. (^) *Eriocaulon setaceum* L., Sp. Pl. 1: 87. 1753.

Eriocaulon melanocephalum Kunth

REF.—Hensold (2014); Oliveira and Bove (2015)

HABITAT—*Mauritia* swamp, submersed in quiet water, 400 m.

DISTRIBUTION—Circumtropical aquatic, described from India; in neotropics, widespread from southern Mexico south to São Paulo, Brazil, and La Paz, Bolivia, east of the Andes. In Peru, only known from Pampas del Heath (MD).

4. *Leiothrix flavescens* (Bong.) Ruhland, Pflanzenr. IV. 30: 231. 1903.

IN PERU—*L. flavescens* var. *flavescens*

HABITAT—In Peru, from wet montane forest openings, on sand or *Sphagnum*; (1100?–) 1800–2500 m. Throughout its range, strongly associated with sand and sandstone or quartzitic outcrops; in Brazil also known from *campo rupestre*, and near sea level in coastal dune formations.

DISTRIBUTION—Amazonian Colombia; Venezuelan Guayana; Guyana; eastern Brazil (Atlantic Forest domain) from Bahia to Rio Grande do Sul; Eastern Andes from Amazonas, Peru to La Paz, Bolivia (Hensold, 2014).

NOTE—Macbride (1936) cites the Puno specimen from 1100 m, but Weberbauer (1945) reports the species from “La Serranía de Yuncacoya ... 1800–2600 m.”

5. *Paepalanthus bifidus* (Schrad.) Kunth, Enum. Pl. [Kunth] 3: 512. 1841.

HABITAT—Wet sandy openings in disturbed forest, roadsides; 1000 m.

DISTRIBUTION—Widespread annual of sandy ground, 0–1200 m; Amazonian Colombia, Venezuela, the Guianas, Amazonian, Central and Northeastern Brazil; in Peru known only from San Martín.

6. **Paepalanthus caryonauta* Hensold, PhytoKeys 64: 16. 2016.

REF.—Hensold (2016)

REGIONS— CU JU PA

HABITAT—Wet páramo; 2900–3900 m.

DISTRIBUTION—Central Cordillera of Colombia and northern Ecuador; disjunctly from Pasco to La Paz, Bolivia.

NOTE—Previously confused with *P. pilosus* and *Eriocaulon microcephalum*.

7. *Paepalanthus crassicaulis* Körn., Fl. Bras. 3(1): 408. 1863. (*Paepalanthus* subg. *Platycaulon*)

REF.—Tissot-Squalli (1997a)

*DISTRIBUTION—Endemic to Amazonas, Prov. Chachapoyas.

8. **Paepalanthus dendroides* (Kunth) Kunth, Enum. Pl. 3: 507. 1841.

REF.—Hensold (2016)

REGIONS— CA CU JU PA PU

HABITAT—Wet páramo or subpáramo, sometimes partly submerged; montane forest margins, seeps, often associated with *Sphagnum*; from 2300–3800 m in Peru; elsewhere known from 1800–3200 m.

DISTRIBUTION—Along the Andes from Costa Rica to Colombia, and in Peru; also disjunct at Pico de Neblina (Venezuela-Brazil border). Expected in Andean Bolivia.

NOTE—Previously treated as a synonym of *P. pilosus*.

9. *Paepalanthus ensifolius* (Kunth) Kunth,
Enum. Pl. 3: 501. 1841.
(*Paepalanthus* subg. *Platycaulon*)

REF.—Tissot-Squalli (1997a)

10. *Paepalanthus ferreyrae* Moldenke, Phytologia 3: 273. 1950.

Paepalanthus wurdackii Moldenke, Phytologia 9: 187. 1963.

HABITAT—Rocky slopes, *jalca*, montane forest margins; 1900–2600 m.

DISTRIBUTION—Endemic. Amazonas: Prov. Bongará; Cajamarca: Prov. Cutervo.

CONSERVATION STATUS—Endangered, Criteria B1ab(iii). The evaluation follows that of Monsalve and León (2006). Additional specimens are known but these are probably from identical localities.

11. (✓) *Paepalanthus glabrescens* (Moldenke) Hensold

Paepalanthus dichotomus var. *glabrescens* Moldenke

HABITAT AND DISTRIBUTION—Endemic to Amazonas, 2300–3100 m. See Taxonomy section above.

CONSERVATION STATUS—Endangered, Criteria B1ab(iii).

12. **Paepalanthus huancabambensis* Hensold,
PhytoKeys 64: 30. 2016.

REF.—Hensold (2016)

REGION— PI

HABITAT—Grass páramo and disturbed cloud forest, 2900–3100 m.

DISTRIBUTION—Endemic to Peru, known only from the type locality near Carmen de la Frontera.

CONSERVATION STATUS—Critically Endangered, Criteria B1ab(iii) (Hensold, 2016).

NOTE—Previously misidentified as *Paepalanthus stuebelianus* or *P. weberbaueri*.

13. (✓) *Paepalanthus intermedius* Körn.,
Fl. Bras. 3(1): 371. 1863.

TYPE: Peru. Amazonas: Chachapoyas, yr 1835, *Fielding misit* in *hb. Fischer* [sine coll.] 1407 (holotype: LE 00001173; probable isotypes, *A. Mathews* 1407: K 000640104, K 000640105, P 00716704).

Paepalanthus stuebelianus Ruhland, Pflanzenr. IV. 30: 174. 1903. TYPE: Peru. Amazonas. “Cuesta de Lejía cerca Molinobamba” [*sphalm.* “Moyobamba” in protologue], 4 Jun 1875. *A. Stübel* 19a (Holotype: B 10 0184173. Isotype: B 10 0184172). **Syn. nov.**

REGION— AM [–PI –SM]

*VOUCHER—*Hutchison & Wright* 5548 (F, MICH, MO, USM)

HABITAT—On seepage areas or marshy sites over sandstone or white sand, in scrub or disturbed evergreen montane forest, often associated with *Sphagnum*; 2000–3200 m.

DISTRIBUTION—*Endemic to Amazonas, Prov. Chachapoyas, in watershed of upper Rio Utcubamba, and Prov. Bongará (see Discussion of *P. piscatorum* in Taxonomy, and Fig. 3).

CONSERVATION STATUS—Vulnerable, Criteria B1ab(iii). Known from 23 confirmed collections, from at least five localities, many recent. The extent of occurrence is about 3500 km².

NOTES—The voucher cited by Brako and Hensold (1993) was a misidentified specimen of *P. huancabambensis* from

Piura. The record from San Martín was based on a transcription error of locality data on the specimen label.

14. **Paepalanthus lodiculoides* Moldenke,
Bull. Torrey Bot. Club 68: 68. 1941.

REF.—Hensold (2016)

REGION— PI

HABITAT—Wet páramo, 3400–4000 m.

DISTRIBUTION—Eastern Cordillera of Colombia, Venezuela (Táchira); disjunct in southern Ecuador and northern Peru.

15. *Paepalanthus longivaginus* Tissot-Squalli, Feddes
Repert. 108: 367. 1997.
(*Paepalanthus* subg. *Platycaulon*)

REF.—Tissot-Squalli (1997b); Ulloa Ulloa et al. (2004)

DISTRIBUTION—Endemic, based on a single collection: Huánuco, Pillao, Ruíz & Pavón s.n. (B, BM, G).

NOTE—Probable duplicates at MA [MA810395; MA810396], annotated with the unpublished name *Eriocaulon vaginans* nom. nud. (Ruíz, 1940), were later distributed as *P. planifolius*.

16. *Paepalanthus obnatus* Tissot-Squalli
(*Paepalanthus* subg. *Platycaulon*)

REF.—Tissot-Squalli (1997b); Ulloa Ulloa et al. (2004)

17. **Paepalanthus paramensis* Moldenke,
Bull. Torrey Bot. Club 68: 69. 1941.
(*Paepalanthus* subg. *Platycaulon*)

REF.—Tissot-Squalli (1997a)

REGION— PA; 2500 m

VOUCHER—*León & Young* 1781 (F)

NOTE—Described from Colombia.

18. *Paepalanthus pilosus* (Kunth) Kunth,
Enum. Pl. 3: 518. 1841.

18a. **Paepalanthus pilosus* var. *leoniae* Hensold,
PhytoKeys 64: 47. 2016.

REF.—Hensold (2016)

REGION— SM

HABITAT—Wet páramo, 3450–3800 m.

DISTRIBUTION—Endemic to Rio Abiseo National Park.

CONSERVATION STATUS—Endangered, Criteria B1ab(iii) (Hensold 2016).

18b. *Paepalanthus pilosus* (Kunth) Kunth var. *pilosus*

REF.—Hensold (2016)

REGIONS— AM *CA [–CU –HU] *LA [–MO] *PI [–PU –SM]

HABITAT—Wet shrubby paramo or *jalca*, wet banks, montane forest, often associated with *Sphagnum*; 3000–3400 m in Peru; 2700–4400 m elsewhere.

DISTRIBUTION—Costa Rica; the Colombian Andes and Cordillera de Mérida, Venezuela; southern Ecuador (Azuay, Loja) and northern Peru.

NOTES—Records of *P. pilosus* from CU, HU, and PU were based on misidentified material of *P. caryonauta* and *P. dendroides*. The record from SM (*León & Young* 1597) is the type of *P. pilosus* var. *leoniae*. The source of the record from Moquegua is unknown and almost certainly incorrect.

19. **Paepalanthus piscatorum* Hensold

IN PERU — *P. piscatorum* var. *piscatorum*

REF.—See Taxonomy section above.

REGIONS — AM CA LO SM

HABITAT AND DISTRIBUTION — Endemic as to variety; (1200–) 1800–2400 m. (See Taxonomy section above.)

CONSERVATION STATUS — Vulnerable, Criteria B1ab(iii).

NOTE — Previously confused with *P. schomburgkii* Klotzsch ex Körn. (Vásquez, 2010). The second variety is known from only one site in southern Ecuador on the Peruvian border, and may be expected in Peru.

20. (?) *Paepalanthus planifolius* (Bong.) Körn.,
Fl. Bras. 3(1): 413. 1863.
(*Paepalanthus* subg. *Platycaulon*)

NOTE — Tissot-Squalli (1997a) provisionally restricted this species to Brazil, and notes that the name has been widely misapplied. One of Macbride's (1936) vouchers is cited in her treatment as *P. crassicaulis*, and another is an isotype of *P. longivaginus*. The identity of the remaining two specimens (HU: *Weberbauer 3535*, and CA: *Raimondi s.n.*, probably both B, destroyed) is unconfirmed.

21. *Paepalanthus weberbaueri* Ruhland,
Bot. Jahrb. Syst. 37: 519. 1906.

HABITAT — Wet open places among shrubs, near tree line in wet dwarf forest of the eastern slope, or “*monte de ceja*,” *sensu* Weberbauer (1945); 1800–2500 m.

DISTRIBUTION — Endemic to Puno, on the eastern slope of the Andes, on a route descending from Sandia to the upper Rio Inambari (Weberbauer, 1904).

CONSERVATION STATUS — Critically Endangered, Criteria B1ab(iii). This distinct species is known from two syntypes, collected in 1902, and preserved in the Berlin herbarium (Röpert, 2000+). The known extent of occurrence of the species is likely less than 100 km, though this remote area of difficult access has been little collected in recent years. Areas of suitable habitat may extend along the eastern slopes, where the species would be expected on sandstone substrates. Threats to the species include a history of placer gold-mining in this area (Weberbauer, 1904).

22. **Syngonanthus androgynus* M. T. C. Watan.,
PLoS ONE e0141187 (5). 2015.

REF.—Watanabe et al. (2015b)

REGION — MD

HABITAT — In sandy wetlands in savanna or cerrado, with *Mauritia*, may be partly submerged; 200 m.

DISTRIBUTION — Central Brazil (Goiás, Minas Gerais), and along the Rio Heath in Bolivia and Peru.

NOTE — Some material was earlier distributed as *S. inundatus* (Körn.) Ruhland. See *S. mollis* notes.

23. *Syngonanthus caulescens* (Poir.) Ruhland,
Bot. Jahrb. Syst. 30(2): 147. 1901.

IN PERU — *S. caulescens* var. *caulescens*

REGIONS — *AM *CA LO *MD SM

VOUCHERS — Amazonas, *Woytkowski 8133* (MO); Cajamarca, *Weigend 98/516a* (F); Madre de Dios, *Beltrán 2397* (USM).

HABITAT — Disturbed openings in forest, swamps, stream-banks, on wet usually sandy sites, sometimes semi-submerged; 220–2000 m.

DISTRIBUTION — Widespread annual in the neotropics from Mexico to Paraguay, east of the Andes.

24. **Syngonanthus davidsei* Huft,
Ann. Missouri Bot. Gard. 72: 448. 1985.

Syngonanthus gracilis var. *aureus* Ruhland, Pflanzenr. IV. 30: 251. 1903.

REF.—Hensold (1999, as *S. gracilis* (Bong.) Ruhland; 2014)

REGION — MD

VOUCHER — *Aguilar & Castro 812* (F, MO, USM)

HABITAT — Wet savannas, cerrados, *morichales*, sandy clay soils of floodplains and riverbanks; 210 m in Peru, 0–1200 (–1500) m elsewhere.

DISTRIBUTION — Widespread annual common throughout South America from Paraguay north to the Caribbean coast, and east to the upper Amazon basin; disjunct in Chiapas, Mexico.

25. *Syngonanthus densiflorus* (Körn.) Ruhland,
Pflanzenr. IV. 30: 263. 1903.

IN PERU — *S. densiflorus* var. *densiflorus*

HABITAT — Savanna and floodplain forest openings on white sands; at 200–400 m in Peru, up to 1200 m in Brazil.

DISTRIBUTION — Central and south Amazonian Brazil, Bolivia, Peru.

26. **Syngonanthus mollis* M. T. C. Watan.,
Phytotaxa 226: 163. 2015.

REF.—Watanabe et al. (2015a)

REGION — MD

VOUCHER — *J. Albán Castillo & R. Foster 6968* (F p.p., USM p.p.)

HABITAT — Terrestrial or emergent aquatic, on sandy savanna floodplain, inundated part of the year, 200 m.

DISTRIBUTION — Known from two collections, one from Santa Cruz, Bolivia, and one from the Río Heath in Peru, in the upper watershed of the Río Madeira.

NOTE — The duplicate at F comprises loose inflorescences only, distributed in mixture with *S. androgynus*. The sheet at USM, observed from a photo, has plants with broader leaves which may represent *S. mollis*. Previously distributed as *S. inundatus*.

27. **Syngonanthus pakaraimensis* Moldenke,
Mem. New York Bot. Gard. 9: 282. 1957.

IN PERU — *S. pakaraimensis* var. *pakaraimensis*

REF.—Hensold (1999)

REGION — PA

VOUCHER — *J. Graham 5439* (F)

HABITAT — In Peru, collected “in sunny waterlogged savanna in dwarf forest over sandstone,” 2000 m; elsewhere at 800–2400 m.

DISTRIBUTION — Common on the Gran Sabana and tepui summits in the highlands of Venezuela (Bolívar) and Guyana; disjunct by 2000 km in Peru, at the Cerro del Sira near the junction with Huánuco and Ucayali regions (Fig. 7).

28. *Syngonanthus peruvianus* Ruhland,
Pflanzenr. IV. 30: 253. 1903.

Syngonanthus yacuambensis Moldenke

REF.—Watanabe et al. (2015a); and see Taxonomy section above.

REGIONS — AM *CA *PA [–SM]

VOUCHERS — Cajamarca, *I. Sánchez Vega 6268* (F); Pasco, *R. Vásquez 30315* (MO)

HABITAT AND DISTRIBUTION—From Azuay Ecuador to Pasco, Peru; 1850–3200 m. See Taxonomy section above.

NOTE—The record from San Martin was based on a label transcription error.

29. **Syngonanthus trichophyllus* Moldenke,
Phytologia 6: 329. 1958.

REF.—Hensold (1999)

REGION— LO

VOUCHERS—*C. del Carpio* 1820 (MO, USM), *L. Torres* 3720 (AMAZ)

HABITAT—Emergent aquatic of streambanks or ephemeral pools in white sand savanna, shrubland; in Peru in inundated blackwater (*igapó*) forest; at 100 m in Peru, 0–1200 m elsewhere.

DISTRIBUTION—Colombia (Caquetá, Vaupés), Rio Apaporis basin; Venezuela (Amazonas, Bolívar); Guyana (Kaieteur Plateau); Brazil (Amazonas), Serra Aracá. The Peruvian records from Loreto in the lower Ucayali drainage extend the distribution by 650 kilometers from Colombia.

30. **Syngonanthus* sp. A

REF.—Hensold (unpublished)

REGION— SM

VOUCHER—*F. Woytkowski* 6204 (LL, MO)

HABITAT—White sand openings in upper montane forest of the eastern slope (*ceja de la montaña*); 1400 m.

DISTRIBUTION—The collection site is southwest of Rioja near the border of San Martín and Amazonas departments, on an “ancient mule trail... [now covered by] an impenetrable thicket.” (See specimen data for *Woytkowski* 6203, Tropicos.org) (Fig. 7).

NOTES—This plant belongs to a difficult complex currently under revision, and may be best treated as an undescribed taxon. It appears intermediate between *Syngonanthus biformis* (N. E. Br.) Gleason and *Syngonanthus simplex* (Miq.) Ruhland, *sensu* Hensold (1999). Similar plants are found in Vaupés, Colombia at about 300 m, in ephemeral pools on sandbanks (e.g., *Schultes & Cabrera* 14963). This specimen was originally distributed as *Syngonanthus compactus* Ruhland ex Ule, a *nomen nudum* originally applied to a different species of Manaus, Brazil (Ule, 1907).

31. *Tonina fluviatilis* Aubl., Hist. Pl. Guiane 2: 857. 1775.

HABITAT—River margins, ditches, swampy ground, often partly submerged or floating; 100–980 m.

DISTRIBUTION—Widespread in neotropics, from West Indies and southern Mexico to Peru, Bolivia, the Guianas, Amazonian and northeastern Brazil.

Taxa Excluded from Peru Checklist

Paepalanthus polytrichoides Kunth

NOTE—This species was recorded from Peru based on a single specimen in the Munich herbarium, which was cited by both Körnicke (1863) and Ruhland (1903). The collection data are given as “Peruvia, *Henschel s.n.*” Henschel didn’t collect in the neotropics, so the specimen is presumably a distribution from his herbarium. It was annotated originally as “*Eriocaulon tenue* Pöpp.,” an unpublished name used by Poeppig in the distribution of his “*Plantae peruviana et amazonicae*.” The Hen-

schel specimen may be a duplicate of *Poeppig* 2983, the type of *P. polytrichoides*, from Pará, Brazil. No other records of this species are known from Peru.

Paepalanthus schomburgkii Klotzsch ex Körn.

REF.—Vásquez and Rodríguez (2002, as “*P. schomburgkiana*”), Vásquez et al. (2010).

NOTE—Based upon misidentified material of *P. piscatorum* Hensold var. *piscatorum*.

Syngonanthus nitens (Bong.) Ruhland

NOTE—Based upon misidentified material of *S. peruvianus* Ruhland.

PART 3. KEY TO THE ERIOCAULACEAE OF PERU

Introductory Notes

The genera of Eriocaulaceae are distinguished by minute floral characters difficult for the non-specialist to interpret, so species are keyed as far as practical by more accessible macro-characters.

The infrageneric taxa *Paepalanthus* subg. *Platycaulon* and *P.* subsect. *Cryptanthella* are not further keyed to species in this key. Keys to species of these groups may be found in the most recent revisions (Tissot-Squalli, 1997a; Hensold, 2016).

As a further aid to identification, a supplementary PDF file, including scans of representative specimens of species included in this checklist, is available online (<http://fieldmuseum.org/fieldiana-hensold>).

The Key

NOTE—Leaf widths were measured at midpoint.

- 1 Capitula compound, each composed of 3 or more tightly congested sub-capitula, each sub-capitulum enclosed by its own involucre of brown bracts, the whole mass borne on a single peduncle dilated at apex. Principal leaves 4–16 mm wide, 3–16 cm long, in rosettes or clumps of rosettes, rarely stems elongating up to 15 cm or more, and then the leaves at least 10 mm wide at midpoint.
.....*Paepalanthus* sect. *Conferti* (Tissot-Squalli, 1997a)
- 1' Capitula simple, each peduncle bearing only one involucre head of flowers; peduncles not apically dilated; involucre white to green, brown or black. Principal leaves 0.25–11 mm wide and 0.15–15 cm long, in rosettes or on elongate stems; if stems elongate, the leaves less than 10 mm wide. 2
- 2 Peduncles borne in terminal umbellate, involucellate clusters of 1–12, on modified leafless or nearly leafless stems. ... 3
- 2' Peduncles borne directly on unmodified leafy stems, in either axillary or terminal position. 4
- 3 Primary stem an unbranched basal rosette of leaves; leaves 7–33 cm long, 3–6 mm wide; modified fertile stem ca. 8–25 cm long, with a few small scale-like leaves scattered along its length and in an involucre at apex; plants of lowland savannas.*Syngonanthus densiflorus*

- 3' Primary stem usually branched near base to form clumps, mats of rosettes, or short erect leafy stems; leaves 1–5 cm long, 0.5–4 mm wide; modified fertile stems less than 3 cm long, naked except for involucre of reduced leaves at apex; plants of montane forest. *Syngonanthus peruvianus*
- 4 Capitula with bracts and flowers all white to pale gold; the surface of the capitulum glabrous or nearly so; sepals never ciliate or plumose at upper margin, though sometimes pubescent on outer surface below the apex, and then the trichomes never surpassing the sepal tips; anthers cream-colored; pistillate or bisexual flowers with petals connate at upper margin. 5
- 4' Capitula with some bracts and/or flowers (sepals) green, brown, copper, gray, or blackish; rarely all cream-colored, but then capitulum surface densely pubescent; anthers cream or black; pistillate flowers with petals free. 14
- 5 Stems short or sometimes elongating up to 5 cm with age, the leaves densely congested in simple or branched basal rosettes, clumps, or mats. 6
- 5' Stems elongate, 3–45 cm long, solitary or sparsely branched at base but rarely above, never in branched mats or clumps, uniformly leafy along their length, the stem usually partially visible between leaf bases. 11
- 6 Capitula conical at maturity, the involucral bracts and floral bracts similar in size; flowers bisexual with a spathaceous fused 2-lobed calyx and 2 petals. Leaves thread-like (capillary), 1.2–6.5 cm long, 0.15–0.25(–0.35) mm wide. Amazonian region, often growing partly submerged in water. *Syngonanthus trichophyllus*
- 6' Capitula campanulate to hemispheric at maturity, floral bracts absent; flowers unisexual, 3-merous, the sepals free at least half their length; Leaves various, 0.5–5.0 cm long, 0.2–4 mm wide. Amazonian to montane forests, on wet sites but rarely submerged. 7
- 7 Mature leaves with adaxial surface villous/villosulous with long filamentous hairs mixed with appressed dibrachiate hairs. 8
- 7' Mature leaves with adaxial surface glabrous or with more or less appressed dibrachiate (malpighian) hairs only, juvenile leaves sometimes hirsutulous (*S. peruvianus*), but never villous, the hairs never long, spreading, filamentous. 9
- 8 Leaves 16–24 mm long, 1–1.2 mm wide; peduncle sheaths ca. 20–30 mm; capitula 5–6 mm diameter; sepals hirsute abaxially below the apex. *Syngonanthus pakaraimensis*
- 8' Leaves 8–20 mm long, 0.25–0.5 mm wide; peduncle sheaths 6–10 mm long; capitula 2.5–4 mm diameter; sepals glabrous. *Syngonanthus* sp. A
- 9 Leaves linear-setaceous, 5–20 mm long, 0.2–0.6 mm wide, in solitary unbranched rosettes; capitula 3–5 mm wide; flowers entirely glabrous; gynoecia with 3 style branches and no nectaries. *Syngonanthus davidsei*
- 9' Leaves lance-linear, 10–50 mm long, 0.6–4.0 mm wide, rosettes various; capitula 3.5–10 mm wide; petals of pistillate flowers pubescent; gynoecia with 3 style branches alternating with 3 clavate nectaries. 10
- 10 Rosettes usually branched, forming clumps; capitula 6–10 mm wide; seeds 0.6–0.7 mm long (also see Lead 12). *Syngonanthus peruvianus*
- 10' Rosettes simple; capitula 3.5–5 mm; seeds 0.35–0.45 mm long (also see Lead 12). *Syngonanthus caulescens* (atypical rosette habit)
- 11 Flowers bisexual, with both stamens and pistil in the same flower; petals inflexed at tip, not fully opening. Leaves 0.25–0.5 mm wide (in Peruvian specimens). *Syngonanthus androgynus*
- 11' Flowers unisexual, the corolla opening at anthesis. Leaves 0.5–4 mm wide. 12
- 12 Capitula 6–10 mm wide. Sepals of staminate flowers conspicuously bearded adaxially near middle with thick straight opaque-white trichomes. Corollas hyaline-membranous throughout. Seeds 0.6–0.7 mm long. Montane forests 2000 m and above. *Syngonanthus peruvianus* (long-stemmed forms)
- 12' Capitula 4–6 mm wide. Sepals of staminate flowers glabrous adaxially or with a few sparse hyaline trichomes within near middle. Corollas spongy-thickened in the bottom half, only the lobes hyaline-membranous; the border between the thickened and membranous zones clearly visible under stereomicroscope when corollas are opened and dissected in water. Amazonian region to montane forests, 0–2000 m 13
- 13 Tips of involucral bracts not surpassing mature capitula; leaves ca. 0.35–1.3 mm wide at midpoint, lance-linear, the apex flat, minutely rounded and sometimes shallowly notched; stems ca 13–45 cm tall. (Seeds not seen.) *Syngonanthus mollis* (Peruvian material)
- 13' Tips of involucral bracts surpassing the mature capitula; leaves mostly ca. 1.5–4.0 mm wide at midpoint, ligulate, the apex minutely conduplicate (canaliculate) and reflexed; stems ca. 1–14 cm tall. Seeds 0.35–0.45 mm long (cf. *S. peruvianus*). *Syngonanthus caulescens* (Peruvian material)
- 14 Plants strongly caulescent with leaves evenly distributed on the stem, the stems 1–160 cm long, sometimes branched at base, but unbranched or loosely branched above, neither with a basal rosette nor forming dense cushions, mats, or clumps. 15
- 14' Plants rosulate or caespitose, the leaves congested in basal rosettes or stems densely branched to form mats, cushions or clumps; branchlets usually less than 4 cm long 19
- 15' Submerged aquatics with long floating, mostly unbranched mucilaginous stems, capitula in terminal fascicles, emergent; leaves capillary, 0.1–0.3 mm wide. Stamens 6 per flower. *Eriocaulon setaceum*
- 15' Plants terrestrial though often on wet ground with trailing stems; stems not mucilaginous; inflorescences terminal or axillary; if plants semi-aquatic, then stems in branched clumps, or capitula solitary in leaf axils. Leaves 0.7–9 mm wide. Stamens 3 per flower. 16
- 16 Stems up to 35 cm long, lax and decumbent with age, rarely branched above base; capitula strictly solitary from leaf axils; peduncles obscure to 12 mm long and horizontally spreading; peduncle sheaths open, leaflike, not tubular, arising adaxially from peduncle base; sepals ciliate or nearly glabrous but not tufted-plumose, stiffly long-acuminate and spreading widely at maturity, the capitulum surface prickly to touch, and never densely soft-pubescent. *Tonina fluviatilis*
- 16' Stems various; capitula terminal, though sometimes displaced laterally with age, erect, solitary to clustered; peduncles 1–150 mm; peduncle sheaths closed, tubular; at least the staminate sepals densely long-ciliate to tufted-plumose at apex; sepal apex obtuse or acute to softly short-acuminate; capitula with soft pubescent surface, not prickly to touch. . 17

- 17 Stems ca. 1–8 cm long at flowering, erect, unbranched below the inflorescence, the naked stem partly visible between the leaf bases; outermost involucre bracts lance-linear, green along the midvein with scarious margins, the sharp tips slightly surpassing the capitulum; peduncles covered with scattered very long soft spreading hairs..... *Paepalanthus bifidus*
- 17' Stems ca. 3–160 cm long at flowering, often decumbent, normally branching just below the inflorescences; the stems covered by the sheathing leaf bases; outermost involucre bracts triangular-ovate, brown, not surpassing the capitulum; peduncles pubescent with short appressed hairs.....28
- 18 Primary stems ca. 24 to 160 cm long at flowering, erect or sprawling, branching 1 to 3 times at apex just below inflorescence, but lower stem usually unbranched; inflorescences in terminal clusters of ca. 5–30 or more; leaves 1.7–6.0 cm long, 2.0–9.0 mm wide at middle, lance-triangular; male corollas with interstaminal lobes ciliate..... *Paepalanthus piscatorum*
- 18' Primary stems usually less than 15 cm at flowering, frequently branched from the base, often densely so, the plants sprawling or forming loose mats; inflorescences terminal, usually 1–2(–5) per node, early overtopped by subterminal branches; leaves 0.5–2.5 cm long, 0.7–3.0 mm wide at middle, varying from narrow-subulate (needle-like) to lance-triangular; male corollas glabrous..... *Paepalanthus intermedius*
- 19 Anthers black, 6 per flower; ovary topped by 3 simple style branches only, otherwise unappendaged; leaves blunt-tipped (but sometimes acuminate), fenestrate at base (i.e., with translucent windows created by air spaces in the mesophyll); peduncles glabrous at apex; involucre bracts broadly rounded at apex, glabrous, hyaline..... 20
- 19' Anthers white to cream-colored, 3 per flower; ovary topped by 3 simple style branches and 3 elongate glandular appendages; leaves blunt to sharp-acuminate, striate but not fenestrate at base; peduncles usually pubescent at apex (except *P. lodiculoides*); involucre bracts obtuse to acuminate, glabrous or pubescent, chartaceous to coriaceous, not hyaline.....21
- 20' Leaves 1–2 cm × 0.9–1.2 mm wide at midpoint; peduncles 1.0–2.4 cm long, 3–4-costate; sheath 8–13 mm; capitula 2.5–4 mm diameter; seed coat reticulate, the anticlinal walls represented by raised membranous strips with an entire margin..... *Eriocaulon microcephalum*
- 20' Leaves 1–14 cm × 1.8–7 mm wide at midpoint; peduncles 1.6–35 cm long, 5–7-costate; sheath 10–85 mm; capitula 4.5–7 mm diameter; seed coat reticulate, the transverse anticlinal walls ornamented with distinct raised knobs (visible with stereomicroscope)..... *Eriocaulon peruvianum*
- 21 Plants simple mostly unbranched rosettes; leaves 4.5–10 cm long, 4–7 mm wide in middle, roots thick white, spongy without a darker fibrous core; peduncles pubescent at apex with a mixture of filamentous and capitate glandular hairs..... *Leiothrix flavescens*
- 21' Plants densely branched cushions, mats or clumps; leaves 1.7–4.0 cm long, 0.25–3 mm wide at middle, roots pale to dark brown, fibrous; peduncles pubescent or glabrous at apex, but never with capitate glandular hairs.....22
- 22 Peduncle sheaths absent; leaves coriaceous, glabrous in the distal half..... *Paepalanthus glabrescens*
- 22' Peduncle sheaths present; leaf texture and pubescence various.....23
- 23 Peduncle sheath mouth glabrous or sometimes minutely tufted at the tip, but never ciliate around the margin; the texture papery-thin, scarious, smooth; frequently splitting into 2–3 triangular segments as buds emerge. *Paepalanthus* subsect. *Cryptanthella* (see Hensold, 2016)
- 23' Peduncle sheath mouth uniformly ciliate at least when young, the texture foliaceous to scarious but then usually veined, not smooth; sometimes splitting with age, but not before inflorescence maturity.....24
- 24 Leaf tips rounded; the leaves linear, 5–10 mm long, the plants forming compact rounded cushions, branchlets mostly 2 cm or less *Paepalanthus ferreyrae*
- 24' Leaf tips sharply acute; the leaves linear to lance-linear, 5–40 mm long, the plants forming loose straggling clumps or mats, not symmetrical rounded cushions; the branchlets 3 cm or more.....25
- 25 Peduncle sheaths 1.2–1.6 cm; peduncles 3.5–9 cm..... *Paepalanthus intermedius* (compact plants)
- 25' Peduncle sheaths 2.0–3.5 cm; peduncles (5.5–)8–27 cm..... *Paepalanthus weberbaueri*

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Appendix I. Index to Numbered Collections

* — Type collection of cited name or synonym.

(PL) — Collections of *Paepalanthus* subg. *Platycaulon* unidentified to species.

p.p. — *pro parte*, i.e., mixed collection with another species

Note: Collections from Ecuador are included for *S. peruvianus*.

Aceto, C. 572 (14).

Aguilar R., M. & D. Castro 532 (25); 812 (24).

Albán C., J. & R. Foster 6968 (22 *p.p.*, 26 *p.p.*); 7004 (25).

Atkin, D. 1 (19); 5A (PL).

Ayala F., F. 265, 1787, 4421, 4447 (31).

Barbour, P. 3427 (18b).

Barclay, H. G. & P. Juajibioy 8500 (28).

Beltrán, H. et al. 1451, 1498 (PL); 2123 (25); 2129 (22); 2397 (23); 2397A (22).

Boeke, J. D. 1815 (13); 1819 (PL); 1825 (28); 1845 (PL); 2034 (28); 2036 (13); 2112 (PL); 2133 (18b).

Boyle, B. et al. 4219 (6); 4869 (PL).

Bussmann, R. et al. 15539, 15542 (13); 17165 (4); 17174 (28); 17189 (13).

Campos, J. et al. 5334 (18b).

Cano, A. 3361 (8); 3872 (6); 3873a (6); 4024 (6); 4437, 4465 (6 *p.p.*, 8 *p.p.*); 5152 (8); 7335 (1); 16840 (18b).

Castro, R., et al. 19593, 19610 (PL).

Chocce, M. et al. 5688 (18b).

Clark, J. L. et al. 11651 (8); 11797 (19).

Croat, T. 58291 (PL).

Davidson, C. 3544 (31).

Del Carpio, C. & J. Ruiz 1820 (29).

Diaz, C. 350 (31); 2832 (PL); 4572 (28); 8951, 8952 (23); 8984 (24); 9201 (22)

Dudley, T. R. 11060, 11194 (6).

Edwin, G. & Schunke 3689 (7)

Epiqueñ, M. 158 (2).

Ferreira, R. A. 809* (10).

Fielding (probably A. Mathews; ex hb. Fischer at LE) 1403* (7); 1407* (13).

Friedberg, C. 256 (14).

Gentry, A. 27685 (31); 39984 (PL); 69772 (3); 69774 (25).

Graham, J. G. 5439 (27); 5530, 6048 (PL).

Hernani, L. 358 (PL)

Holm-Nielsen, L. B. et al. 4814, 5080 (28).

Hormia, K. 2055, 2081 (31).

Huamantupa, I. 4480 (6).

Hutchison, P. C. & J. K. Wright 5541 (7); 5548 (13); 5556 (28).

Jørgensen, P. 449 (28).

Killip, E. P. & A. C. Smith 28683 (23).

Klug, G. 2866, 3270 (23)

Knapp, S. et al. 7440 (23); 7455 (31).

Lechler, W. (ed. Hohenacker) 2206 (8).

Leiva, S. et al. 1370 (2).

León, B. 960 (PL); 1883 (1); 1597* (18a); 1781 (17); 2243 (8); 2245, 2431 (6); 2683 (8); 4579 (18a); s.n. [USM111244] (8).

López M., A. & A. Sagástegui 5347 (PL).

Luteyn, J. L. & M. Lebrón-Luteyn 5525 (4); 5526 (13); 5532 (PL)

Macbride, J. F. 5182 (8).

Mathews, A. 1405 (2). Possible isotype, holotype at BR unnumbered.

Mathews, A. (Fielding *misit*) 1403* (7); 1407* (13)

McDaniel, S. 10744, 16543, 20534, 21619 (31).

Monteagudo Mendoza, A. et al. 4598, 7177, 7216, 7460, 7904 (PL); 7938 (hybrid 6 × 8); 12833 (PL); 16143 (6); 16530 (28).

Mostacero, J. et al. 1594 (10); 1598, 1635 (9)

Neill, D. & W. Quizhpe 15235* (type of *Paepalanthus piscatorum* var. *ecuadorensis*).

Núñez, P. 7773 (6 *p.p.*, 8 *p.p.*).

Ochoa T., H. 13 (14).

Pennell, F. W. 13864 (6); 13866 (8); 15723 (13 *p.p.*, 28 *p.p.*); 15756 (13); 15769 (28); 15770 (13).

Perea, J. et al. 660 (PL); 3629 (19).
Peyton, B. & S. Tilney Peyton 914 (6).
Prieto, F. P-197* (28, type *S. yacuambensis*).
Quipuscoa, V. 1361 (28).
Rauh, W. 40320 (28); 40321 (13); 62785 (2); 63709 (28); 63752 (19); 63766 (28); 63775 (13).
Revilla, J. 3509 (31).
Rios, M. et al. 3303 (19).
Rodríguez R., E. 1821, 2769 (PL).
Rojas, R. 1552 (PL); 2261 (4); 2278 (PL); 3171 (19); 3293, 3398, 3650 (PL); 3654 (4).
Ruiz & Pavón s.n. [MA-810392, MA-810393, MA-810394; MO-1612102] (8); s.n.* [MA-810395, MA-810396] (15)
Sagástegui, A. 6062 (28); 7454 (11); 10225 (12); 12242 (18b); 16799* (12).
Sanchez Vega, I. 4461 (9); 4597 (2); 6268 (28); 6341 (9); 8131 (PL); 10020 (10).
Santa Cruz, L. 653, 2018 (8).
Smith, D.N. 2528 (PL); 4150 (28); 4822 (19); 5006 (28); 5006A (13); 5892, 8191 (PL).
Spichiger, R. E. et al. 1437 (31).
Stork, H. E. & O. B. Horton 10122 (9)
Stübel, A. 19a* (13); 19b* (28).
Torres, Luis et al. 3720 (29).
Tovar, O. et al. 1370 (31).
Tupayachi, A. 50 (8).
Valenzuela Gamarra, L. et al. 8117* (6); 13442 (PL); 13444 (28).
van der Werff, H. et al. 8537, 8531 (PL); 14839 (13); 14862 (PL); 14888 (13); 14905 (4); 14916 (PL); 14940 (11); 14978 (13); 15070 (28); 15089 (4); 15263 (PL); 15706 (19); 16506 (23); 16517 (5); 16531 (5); 16719 (19); 16751, 16896 (PL); 16912 (11); 16915, 16920 (13); 16920A (28); 17571, 17585 (PL); 17591 (4); 18671, 18718, 19650, 19774 (PL); 25237 (13); 25239 (PL); 25259 (28); 25282 (hybrid? 19 × 13); 25465 (PL); 25546 (4); 25547 (28); 25563 (13); 25580 (13).
Vásquez-M., R. 10269, 16744 (31); 21996 (18b); 24602 (19); 26586 (PL); 26788 (7); 27787, 28551 (PL); 29031 (1); 29038 (8); 30005 (PL); 30315 (28); 31422 (4); 31432, 31508, 31899, 34501 (PL).
Vera 1567 (4).
Vilca, S. 179, 491 (PL).
Weberbauer, A. 1152* (21, syntype); 1292 (4); 1326* (21, syntype); 4328 (28); 4351 [4531?] (7); 4416 (18b); 4565 (23); 4607 (5).
Weigend, M. 97/82, 97/83, 97/425 (PL); 98/252 (12); 98/371 (28); 98/395 (13); 98/396 (PL); 98/416 (4); 98/417 (13); 98/498* (19); 98/506 (PL); 98/516a (23).
Williams, L.I. 7571 (13).
Woytkowski, F. 567 (8); 6204 (30); 8133 (23); s.n. [USM 15173] (23).
Woytkowski, F. [Goodspeed Expedition] 34070 (PL); 34117 (1); 35330 (23).
Wurdack, J. J. 514 (2); 583 (4); 1000 (16); 1081* (10); 1337 (13); 1338 (28); 1358 (13); 1379 (28); 1388* (11); 1616 (18b); 1741 (13).
Young, K. & B. León 4368 (18a); 4790 (1).

Index to Scientific Names

Synonyms are in *italics*

Bromeliaceae

Comanthera L. B. Sm.
Comanthera L. B. Sm. subg. Comanthera
Eriocaulon brachypus Bong.
Eriocaulon brachypus van Heurck & Müll. Arg.
Eriocaulon melanocephalum Kunth
Eriocaulon microcephalum Kunth
Eriocaulon peruvianum Ruhland
Eriocaulon setaceum L.
Eriocaulon tenue Poeppig, ined.
Eriocaulon truncatum Mart.
Eriocaulon vaginans Ruíz, nom. nud.
Leiothrix flavescens (Bong.) Ruhland
Paepalanthoideae Ruhland
Paepalanthus Mart.
Paepalanthus sect. Conferti (Ruhland) Tissot-Squalli ex Hensold
Paepalanthus sect. Divisi (Ruhland) Tissot-Squalli ex Hensold
Paepalanthus sect. Dyostiche Ruhland
Paepalanthus subg. *Andraspidopsis* Körn.
Paepalanthus subg. Monosperma Hensold
Paepalanthus subg. Platycaulon Körn.
Paepalanthus subg. *Psilocephalus* Körn.
Paepalanthus subg. Xeractis Körn.
Paepalanthus subsect. Cryptanthella Suess.
Paepalanthus subsect. Dichocladus Ruhland
Paepalanthus subsect. Polyactis Ruhland
Paepalanthus aristatus
Paepalanthus bifidus (Schrad.) Kunth
Paepalanthus bonsai Trovó & Sano
Paepalanthus caryonauta Hensold
Paepalanthus crassicaulis Körn.
Paepalanthus dendroides (Kunth) Kunth
Paepalanthus dichotomus Klotzsch ex Körn.
Paepalanthus dichotomus var. *glabrescens* Moldenke
Paepalanthus distichophyllus Mart.
Paepalanthus elongatus (Bong.) Körn.
Paepalanthus ensifolius (Kunth) Kunth
Paepalanthus ferreyrae Moldenke
Paepalanthus glabrescens (Moldenke) Hensold
Paepalanthus glaziovii Ruhland
Paepalanthus huancabambensis Hensold
Paepalanthus intermedius Körn.
Paepalanthus lamarckii Kunth
Paepalanthus lodiculoides Moldenke
Paepalanthus longivaginatus Tissot-Squalli
Paepalanthus muscosus Körn.
Paepalanthus obnatus Tissot-Squalli
Paepalanthus paramensis Moldenke
Paepalanthus pilosus (Kunth) Kunth
Paepalanthus pilosus var. *leoniae* Hensold
Paepalanthus pilosus var. *pilosus*
Paepalanthus piscatorum Hensold
Paepalanthus piscatorum Hensold var. *piscatorum*
Paepalanthus piscatorum var. *ecuadorensis* Hensold
Paepalanthus planifolius (Bong.) Körn.
Paepalanthus polytrichoides Kunth
Paepalanthus schomburgkii Klotzsch ex Körn.
Paepalanthus sessiliflorus Körn.
Paepalanthus stannardii Giul. & L. R. Parra
Paepalanthus stuebelianus Ruhland
Paepalanthus trichopetalum Körn.
Paepalanthus weberbaueri Ruhland (1906)

Paepalanthus wurdackii Moldenke
Rondonanthus acopanensis (Moldenke) Hensold & Giul.
Syngonanthus Ruhland
Syngonanthus sect. *Carphocephalus* (Körn.) Ruhland
Syngonanthus sect. *Dimorphocaulon* Ruhland
Syngonanthus sect. *Syngonanthus*
Syngonanthus sp. A
Syngonanthus androgynus M. T. C. Watan.
Syngonanthus biformis (N. E. Br.) Gleason
Syngonanthus caulescens (Poir.) Ruhland
Syngonanthus compactus Ruhland ex Ule, nom. nud.
Syngonanthus cuyabensis (Bong.) Giul. et al.
Syngonanthus davidsei Huft

Syngonanthus densiflorus (Körn.) Ruhland
Syngonanthus fischerianus (Bong.) Ruhland
Syngonanthus gracilis var. *aureus* Ruhland
Syngonanthus mollis M. T. C. Watan.
Syngonanthus nitens (Bong.) Ruhland
Syngonanthus pakaraimensis Moldenke
Syngonanthus pakaraimensis Moldenke var. *pakaraimensis*
Syngonanthus peruvianus Ruhland
Syngonanthus simplex (Miq.) Ruhland
Syngonanthus trichophyllus Moldenke
Syngonanthus yacuambensis Moldenke
Tonina fluviatilis Aubl.
Trichomanes L.



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